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Implications of land-use change and pasture management on soil microbial function and structure in the mountain rainforest region of southern Ecuador

(Einfluss der Landnutzungsänderung und des Weidemanagements auf Funktion und Struktur der Bodenmikroorganismen in einer Bergregenwaldregion im Süden von Ecuador)

(Efectos del cambio de uso de la tierra y del manejo de pastos sobre la función y estructura de los microorganismos del suelo en la región de bosques tropicales montañosos en el Sur de Ecuador)

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Dipl. Geogr. Karin Potthast

Gutachter:

Herr Prof. Dr. Franz Makeschin
Technische Universität Dresden/ Lehrstuhl für Bodenkunde und Bodenschutz
Herr Prof. Dr. Rainer Jörgensen
Universität Kassel/ Fachgebiet Bodenbiologie und Pflanzenernährung
Herr Prof. Dr. Gert Dudel
Technische Universität Dresden/ Lehrstuhl für Allgemeine Ökologie

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Die Übereinstimmung dieses Exemplars mit dem Original der Dissertation zum Thema:

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To my father

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Abbreviations

asl	above sea level
C_3 plant	plant with the C_3 pathway of photosynthesis
C_4 plant	plant with the C_4 pathway of photosynthesis
CEC	cation exchange capacity
CFE	chloroform fumigation–extraction
$\delta^{13}C$	$^{13}C/^{12}C$ ratio expressed relative to Vienna PDB standard
DFG	Deutsche Forschungsgemeinschaft
DM	dry matter
DOC	dissolved organic carbon (KCl extractable)
DOM	dissolved organic matter
DON	dissolved organic nitrogen (KCl extractable)
EA-IRMS	elemental analyzer-isotope ratio mass spectrometry
EGM	environmental gas monitor
ESCF	Estación Científica San Francisco
FERPAST	pasture fertilization experiment
ICP-OES	inductively coupled plasma optical emission spectrometry
IRGA	infrared gas analyzer
MBC	microbial biomass carbon
MBN	microbial biomass nitrogen
MBP	microbial biomass phosphorus
n	number of replicates
OM	organic matter
PDB	PeeDeeBelemnite, standard for ^{13}C-analysis
PE	priming effect
PLFA	phospholipid fatty acid
PO_4-P	phosphate P (NH_4-F extractable)
r	correlation coefficient
RDA	redundancy analysis
SE	standard error
SOC	soil organic carbon
SOM	soil organic matter
TDN	total dissolved nitrogen (KCl extractable)
TN	total nitrogen
TP	total phosphorus
NH_4-N	ammonium N (KCl extractable)
NO_3-N	nitrate N (KCl extractable)
WRB	world reference base for soil resources

Summary

In the present thesis, implications of pasture establishment, fertilization and abandonment on soil C and nutrient dynamics were investigated for the mountain rainforest region of southern Ecuador. Over the past decades the natural forest of the study area has been threatened by conversion to cattle pastures. However, the soil fertility of these extensively grazed pastures (active pastures) declines continuously during pasture use. The invasion of bracken fern (*Pteridium arachnoideum*) leads to pasture abandonment when bracken becomes dominant. In order to reveal the mechanisms behind the deterioration of soil fertility, biotic and abiotic soil properties and their interaction were analyzed along a land-use gradient (natural forest – active pasture – abandoned pasture).

The ecosystem disturbance of the mountain rainforest through pasture use changed the microbial function and structure, and affected soil CO_2-C fluxes. Annually, 2 Mg soil CO_2-C ha^{-1} were additionally emitted from the pasture land. This acceleration in soil respiration rates was related to accelerated rates of microbial C mineralization and fine-root respiration. The high-quality, N-rich above- and belowground residues of the pasture grass (*S. sphacelata*, C_4-plant), especially the huge fine-root biomass, provided a high C and N availability for soil microbes. Compared to the forest, increased soil pH and accelerated base saturation were further factors beneficial for soil microbial growth and metabolism of the upper mineral soil at active pastures. Three times higher amounts of microbial biomass C and a significant shift in the microbial community structure towards a higher relative abundance of Gram(-)- bacteria and fungi were observed.

Long-term pasture use and the invasion of bracken (C_3-plant) diminished beneficial effects for microbes, causing a significant decrease in the C, net, and gross N mineralization rates as well as a two-third reduction in the microbial biomass. A preferential substrate utilization of grass-derived C_4 by the soil microbes resulted in a rapid decline of the C_4-pool. As a consequence, the less available C_3-pool from bracken and former forest increased its dominance in the SOC-pool, further decreasing pasture productivity and finally causing pasture abandonment. The lower quality and quantity of above- and belowground residues of the bracken (high lignin content, C/N) resulted in resource-limited conditions that influenced the microbial function to greater extent than their structure. The microbial structure seemed to be sensitive mainly to soil pH along the land-use gradient. Thus, a disconnection between microbial structure and function was identified.

Fertilization experiments were conducted both in the lab and in the field to evaluate the impact of urea and/or rock phosphate amendment on SOM dynamics and on pasture productivity of active pastures. After combined fertilization the pasture yield was most efficiently increased by 2 Mg ha^{-1} a^{-1}, indicating a NP-limitation of grass growth. Furthermore, the fodder quality was improved by a higher content of P and Ca in the grass biomass. The microorganisms of the active pasture soil responded with an adaptation of their structure to the increased substrate availability in the short term, but did not change their initial functions in the long term. After urea/ rock phosphate addition a significant increase in the relative fungal abundance was detected, but neither a microbial limitation of

energy nor of N or P was observed. However, urea addition accelerated gaseous losses of soil CO_2-C in the short term.

In the study area, pronounced alterations in ecosystem functioning due to land-use changes were detected, especially in soil C and N cycling rates. For a sustainable land-use in this region it is crucial to prevent pasture degradation and to rehabilitate degraded pastures in order to protect the prevailing mountain rainforest ecosystem. It is of crucial importance for active pasture soils to maintain or even increase resource availability, being one indicator of soil fertility. In this context, the soil organic matter has to be retained in the long-term to maintain high microbial activity and biomass, and thus pasture productivity. A moderate fertilization with urea and rock phosphate can be a first step to provide continuous nutrient supply for grass growth and to strengthen livestock health through increased fodder quality. However, the risk of further additional emissions of soil CO_2-C due to increased loads of urea fertilizer application has to be kept in mind. Overall, for the establishment of a sustainable land-use management the control of bracken invasion and an adjusted nutrient management are needed. Further investigations on the reduction of soil nutrient losses and increased nutrient use efficiencies of plants, such as combined planting with legumes or the usage of cultivars with special nutrient acquisition strategies, should be in the focus of future work.

Zusammenfassung

In der vorliegenden Dissertation werden die Auswirkungen der Weideetablierung, -düngung sowie des Verlassens von Weiden auf Bodenkohlenstoff- und Nährstoffdynamik in einer tropischen Bergregenwaldregion Ecuadors zusammenfassend dargestellt und diskutiert. Der Naturwald des Untersuchungsgebietes ist seit Jahrzehnten durch Brandrodung und die Umwandlung in extensiv genutztes Weideland (aktive Weide) in seinem flächenhaften Bestand bedroht. Als Problem hat sich der Verlust an Fruchtbarkeit der Weideböden während ihrer Bewirtschaftung herausgestellt. Des Weiteren führt die Einwanderung des Tropischen Adlerfarns (*Pteridium arachnoideum,* C_3-Pflanze) zu einer Reduktion der oberirdischen Grasbiomasse. Nimmt diese Entwicklung überhand, werden die betroffenen Flächen von den Bauern nicht mehr aktiv genutzt, verlassen und neuer Regenwald gerodet. Um mehr über die Mechanismen der Verringerung der Bodenfruchtbarkeit zu erfahren, wurden biotische und abiotische Bodeneigenschaften und deren Interaktion entlang eines Landnutzungsgradienten (Naturwald – aktive Weide – verlassene Weide) untersucht.

Die Zerstörung des Bergregenwaldökosystems und die Überführung der gerodeten Flächen zur Weidebewirtschaftung verändert die Funktion und Struktur der Bodenmikroorganismen und beeinflusst den CO_2-C Fluss aus dem Boden. Jährlich werden 2 t CO_2-C ha^{-1} zusätzlich vom Weideland emittiert. Diese Erhöhung der Bodenatmungsraten kann mit erhöhten Raten der mikrobiellen C-Mineralisierung und Feinwurzelatmung in Verbindung gebracht werden. Das Weidegras (*S. sphacelata*, C_4-Pflanze) liefert C- und N-reiche ober- und unterirdische organische Substanz (z.B. durch die Feinwurzelbiomasse) und trägt damit zu einer Erhöhung der C- und N-Verfügbarkeit für die Mikroorganismen bei. Darüber

hinaus stellen ein höherer pH-Wert und eine erhöhte Basensättigung im oberen Mineralboden der aktiven Weide günstige Bedingungen für mikrobielles Wachstum und Metabolismus dar. Als Konsequenz sind die Gehalte an mikrobiellem Biomassekohlenstoff um das Dreifache erhöht und die mikrobiellen Gemeinschaftsstrukturen signifikant in Richtung einer höheren relativen Abundanz der Gram(-)-Bakterien und Pilze verschoben.

Eine längerfristige Weidebewirtschaftung ohne Kompensation von Nährstoffverlusten sowie die Einwanderung des Tropischen Adlerfarnes verschlechterte die Bedingungen für die Mikroorganismen, was zu einem signifikanten Rückgang des SOC, der Netto- und Brutto-N-Mineralisierungsraten sowie zu einer Halbierung der mikrobiellen Biomasse führt. Eine bevorzugte Substratnutzung von Graskohlenstoff (C_4) durch die Mikroorganismen hat einen schnellen Abbau des C_4-Pools zur Folge. Somit dominiert nun der mikrobiell schlechter verfügbare C_3-Pool den Bodenkohlenstoffpool. Dies führt zu einem weiteren Rückgang der Weideproduktivität und schließlich zum Offenlassen der Weide. Die geringere Qualität und Quantität der vom Farn stammenden ober- und unterirdischen organischen Substanz (hoher Ligninanteil, weites C/N), führten zu einer Limitierung der Ressourcen für die Mikroorganismen, welche deren Funktionen in größerem Maße beeinflussen als deren Gemeinschaftsstruktur. Im Gegensatz dazu wird entlang des Landnutzungsgradienten die Struktur hauptsächlich durch den pH-Wert beeinflusst. Daraus folgt, dass Struktur und Funktion der Bodenmikroorganismen voneinander entkoppelt auf Veränderungen reagieren können.

Um den Einfluss von Harnstoff- und/ oder Rohphosphatdüngung aktiver Weiden auf die Dynamik der organischen Bodensubstanz und auf die Weideproduktivität zu untersuchen, wurden sowohl Labor- als auch Feldversuche durchgeführt. Im Feldexperiment wurde gezeigt, dass eine NP-Limitierung der Grasbiomasseproduktion vorliegt und durch eine geringe NP-Kombinationsdüngung die oberirdische Phytomasseproduktion um 2 t ha^{-1} a^{-1} gesteigert und die Futterqualität durch eine Erhöhung der P- und Ca- Gehalte verbessert werden kann. Die Mikroorganismen reagierten mit einer Anpassung ihrer Struktur an die kurzzeitig erhöhte Substratverfügbarkeit. Nach Gabe von Harnstoff und/ oder Rohphosphat wurde weder eine N- noch eine P-Limitierung der Bodenmikroorganismen festgestellt, und die mikrobiellen Funktionen wurden langfristig nicht verändert. Dagegen bewirkte die Düngergabe einen erhöhten relativen Anteil der Pilzabundanz. Im Labor sowie im Feld kam es nach Harnstoffdüngung kurzzeitig zu verstärkten gasförmigen Verlusten des Bodenkohlenstoffs.

Aufgrund der Landnutzungsänderungen im Untersuchungsgebiet veränderten sich die Ökosystemfunktionen stark, speziell die Boden-C- und Boden-N-Umsatzraten. Für eine nachhaltige Landnutzung in der Region, d. h., für den Schutz der noch verbliebenen natürlichen Bergregenwaldflächen, ist es von entscheidender Bedeutung, dass die Weidedegradierung verhindert wird und degradierte Flächen wieder in Nutzung genommen werden. Als entscheidend für die Weideproduktivität hat sich in dieser Studie die Ressourcenverfügbarkeit für Bodenmikroorganismen herausgestellt. Daher ist es sehr wichtig, diese Ressourcenverfügbarkeit in Böden aktiv-genutzter Weiden zu erhalten oder noch zu erhöhen, denn sie wirkt sich vor allem auf die organische Bodensubstanz und im Wechselspiel damit auf die mikrobielle Biomasse und Aktivität aus. Eine moderate Kombinationsdüngung aus Harnstoff und Rohphosphat ist ein erster Schritt in diese Richtung. Dabei sollte jedoch das Risiko zusätzlicher bodenbürtiger CO_2-C Emissionen in Folge höherer Düngergaben be-

rücksichtigt werden. Für ein nachhaltiges Landnutzungsmanagement sind Maßnahmen gegen die Einwanderung des Adlerfarnes und ein angepasstes Nährstoffmanagement notwendig. Weitere Untersuchungen sollten auf eine Minimierung der Nährstoffverluste und eine erhöhte Nährstoffnutzungseffizienz der Pflanzen fokussiert werden. Weidemischkulturen aus Gräsern mit Leguminosen sowie der Einsatz von Kulturen mit speziellen Nährstoffaneignungsstrategien könnten dabei eine große Rolle spielen und sollten in der Region erprobt werden.

Resumen

La tesis presentada investiga el impacto del establecimiento de pasto, de su fertilización y de su manejo tradicional (abandono del pastizal) a la dinámica del carbono y de los nutrientes de suelo en la región de los bosques tropicales montañosos en el Sur de Ecuador. Durante las últimas décadas el bosque natural en el área de estudio ha estado amenazada por su conversión a pastizales. Sin embargo, la fertilidad del suelo en pastos de tipo extensivo (pastos activos) decrece frecuentemente durante el uso de los pastos. La invasión de Llashipa (*Pteridium arachnoideum*) conduce al abandono de los pastos cuando la ésta se vuelve dominante. Con la finalidad de revelar los mecanismos detrás de esta disminución de la fertilidad de suelo, se analizaron las propiedades bióticas y abióticas del suelo y sus interacciones, a lo largo de una gradiente del uso de la tierra (bosque natural — pasto activo — pastos abandonados).

La perturbación del ecosistema de bosque tropical montañoso por su cambio de uso, mediante el establecimiento de pastizales, ha alterado la función y la estructura de los microorganismos y ha afectado el flujo de CO_2-C del suelo. Cada año 2 Mg CO_2-C ha^{-1} fueron emitidas adicionalmente por el establecimiento de pastos. Esta aceleración en la tasa de respiración del suelo está relacionada con el aumento de las tasas de mineralización microbiana de carbono y de la respiración de las raíces. La alta calidad y abundancia de N de los residuos orgánicos del suelo con pasto Mequeron (*S. sphacelata*, C_4-planta), especialmente debido a la gran biomasa de las raíces finas, ofrecen una disponibilidad alta de C y N para los microorganismos. En comparación con el bosque natural, el aumento del pH y la saturación bases acelerada fueron condiciones más favorables para el crecimiento microbiano y para el metabolismo microbiano en el parte superior del suelo mineral en pastos activos. La cantidad de C de la biomasa de los microorganismos fue tres veces mayor que la del bosque y se ha observado un cambio significativo de la estructura de la comunidad microbiana, en donde la abundancia relativa de los hongos y de las bacterias Gram(-) ha aumentado.

El uso de pasto a largo plazo y la invasión de Llashipa (C_3-planta) han reducido los efectos benéficos para los microorganismos, que resultaron en una reducción significativa de las tasas de la mineralización de C y N, y en una reducción en dos tercios de la biomasa microbiana. El uso preferencial de los microorganismos por sustrato de pasto C_4 han resultado en una rápida disminución de la reserva de C_4. Como consecuencia, la menor disponibilidad de la reserva de C_3 de las plantas de Llashipa y de la cobertura anterior de bosque ha incrementado su dominancia en la reserva de materia orgánica del suelo. Eso

resulta, en una mayor disminución de la productividad de los pastos, conduciendo finalmente al abandono de los campos de pastos. La menor calidad y cantidad de los residuos acumulados sobre y bajo el suelo provenientes de la Llashipa han dado como resultado un sustrato de limitadas condiciones que están afectando más a las funciones microbiales antes que a su estructura. La estructura microbiana parece ser más sensible al pH del suelo a largo de la gradiente del uso de la tierra; de manera que se ha identificado una desconexión entre la estructura y función microbial.

Experimentos de fertilización en laboratorio y en campo han sido realizados para evaluar el impacto de la aplicación de enmiendas (urea y/o roca fosfórica) a la dinámica de la materia orgánica y a la productividad de los pastos activos. El resultado del experimento de campo ha demostrado que la fertilización combinada es más efectiva, mostrando un aumento en la producción de biomasa de 2 Mg ha^{-1} a^{-1}, lo que indica una limitación de N y P para el crecimiento del pasto. Además, la calidad de forraje se mostró incrementada ya que el contenido de P y de Ca han aumentado significativamente. Los microorganismos del suelo en el pasto activo han respondido a corto plazo con una adaptación de su estructura ante la disponibilidad de sustrato, pero no han mostrado un cambio de sus funciones iniciales a largo plazo. Después de la aplicación de urea y de la roca fosfórica, se detectó un incremento significativo en la abundancia de los hongos, pero tampoco se observó una limitación de energía microbial ni de N o P. Sin embargo, la aplicación de urea ha aumentado la pérdida gaseosa de CO_2-C del suelo a corto plazo.

Debido al cambio de uso de la tierra en la área de investigación, se ha detectado una alteración notable de la función del ecosistema, especialmente en el ciclo de C y N de suelo. Para un uso sostenible de la tierra en esta región, es crucial el prevenir la degradación de pastos y rehabilitar aquellos degradados. En el suelo de pastos activos es de gran importancia el mantener o aún mejor el aumentar la disponibilidad del sustrato, que es uno de los indicadores de la fertilidad del suelo. En este contexto, la materia orgánica se debe ser retenida a largo plazo para mantener la actividad y biomasa microbiana alta y por ende la productividad de pasto. Una moderada fertilización con urea y roca fosfórica puede ser un primer paso para proveer un continuo suministro de nutrientes por el crecimiento del pasto y para reforzar la sanidad pecuaria por medio de un forraje de mayor calidad. Sin embargo, el riesgo de emisiones adicionales de CO_2-C del suelo debido a una aplicación más alta de urea debe tenerse en cuenta. Se puede concluir que para un manejo sostenible del uso de la tierra, tanto el control de la invasión de Llashipa y como un suministro adecuado de nutrientes son necesarios. Adicionalmente se podría decir que es necesario profundizar el estudio de la reducción de las pérdidas de los nutrientes de suelo y de la eficiencia del uso de los nutrientes en las plantas, así como las asociaciones de pastos con leguminosas o el uso de cultivos de absorción selectiva de nutrientes, que serían estrategias importantes para el futuro.

1 Introduction

1.1 Impact of land-use changes on C and nutrient dynamics

The function of ecosystems can be altered substantially by global land-cover and land-use changes through modifications in above- and belowground processes (Berthrong *et al*., 2009; Chapin III *et al.*, 2009; Macdonald *et al*., 2009; Verchot, 2010; Wolters *et al*., 2000). 80% of the terrestrial vegetation cover is assumed to be altered by human impact (Chapin III *et al*., 2009), mainly as a result of the conversion of natural forest to agricultural land for food production (Bardgett, 2011). Global deforestation rates are slowing down slightly, whereas deforestation of humid tropical forests is still proceeding on a large scale at the expense of biodiversity and of CO_2-losses to the atmosphere (FAO, 2010; IPCC, 2007). Inappropriate land-use management together with the invasion of competitive plant species into agricultural land can cause further loss of biological productivity and finally abandoned wasted land (Dias-Filho *et al*., 2001). As a consequence, the process of natural forest clearance and fragmentation continues, and species are threatened or face extinction, especially in species-rich regions of the world, such as Southeast Asia, Central America, and the tropical forests in South America (Sala *et al*., 2000; Wardle *et al*., 2011). This biotic impoverishment of ecosystems has considerable consequences for global

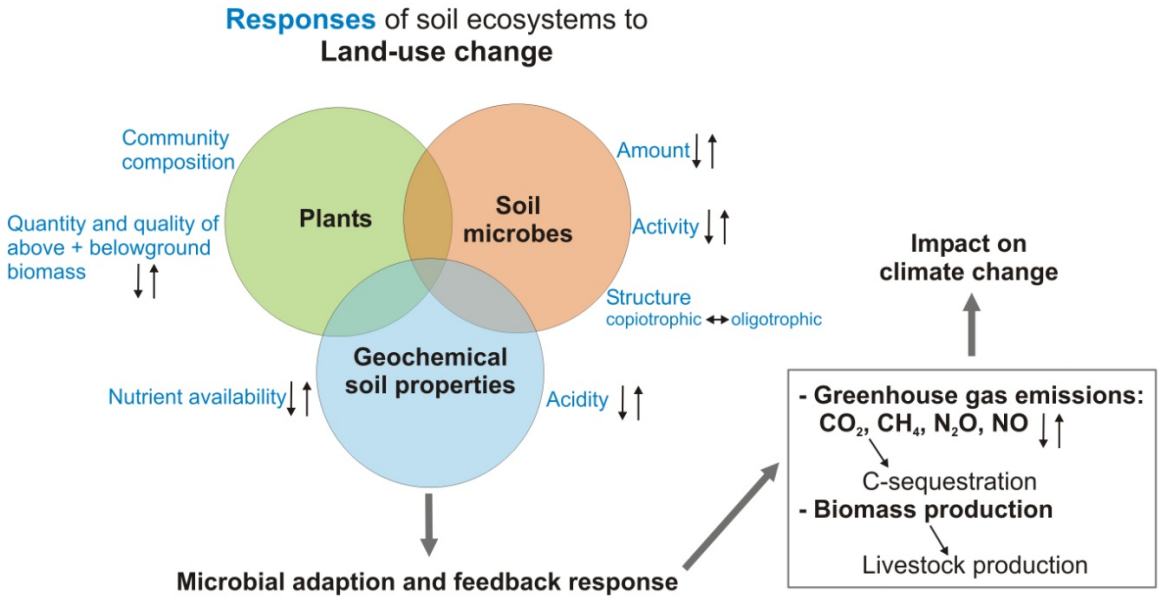


Figure 1.1: Feedback responses of soil microbes to global changes and their interactions with plants and geochemical soil properties. Microbial adaption and feedback response to land-use changes control greenhouse gas emissions and biomass production.The control mechanisms of the microbes are still not fully understood. Figure adapted from Singh *et al.* (2010).

changes through the alteration of a complex network of interacting feedbacks between organisms and their abiotic environment (Fig. 1.1) changing terrestrial C dynamics (Bardgett and Wardle, 2010; Singh *et al*., 2010).

Deforestation of tropical forests and intensive agriculture contribute to large losses of C and nutrients from the ecosystem (McLauchlan, 2006). Particularly in the humid tropics, land-use changes have a great impact on soil geochemical properties (Townsend *et al*., 2002) since highly weathered soils with low inherent fertility, strong acidity and high portion of iron and aluminum clays prevail (Nortcliff, 2010). C and nutrients of these soils can be lost rapidly by (i) burning of forest residues, (ii) biomass harvest and livestock emissions as well as by (iii) leaching and erosion processes right after clearing due to lacking vegetation cover and high precipitation (Chapin *et al*., 2002; IPCC, 2007; Veldkamp *et al*., 2008). While a short-lived increase in nutrient availability can be detected directly after burning, long-term nutrient depletions often occur (Townsend *et al*., 2002). The availability of P for microbes and plants was found to decrease during agricultural use since P-sorption capacity increased and atmospheric inputs of P are low (Cleveland *et al*., 2003; Townsend *et al*., 2002). In contrast to P, as the most limiting element in humid tropical soils (Cleveland *et al*., 2002), possible N losses through NO_3-N leaching and gaseous emissions (N_2O, NO_x) (Neill *et al*., 2006) can be compensated by atmospheric N inputs by N deposition or N_2-fixating bacteria.

Largest land-to-atmosphere CO_2 emissions were caused by slash and burn of natural forest. In the 1990s the approximate net annual land-use flux of the tropics accounted for about 2.2 ± 0.8 Gt C (±SD), whereas total non-tropics accounted for a slight uptake of C by reforestation and agricultural abandonment (-0.02 ± 0.8 Gt C a^{-1}) (Houghton, 2003). Global climate change is amplified by increased soil trace gas emissions (CO_2, CH_4, N_2O, NO_x) through fire, enhanced decomposition and vegetation change (IPCC, 2007). 12-20% of the human-induced trace gas emissions originate from land-use changes in the tropics and are not expected to decrease in the future due to continuing population growth (Amundson, 2001; IPCC, 2007).

1.1.1 Soil organic carbon and soil CO_2 flux

A central function of ecosystems is the sequestration of organic C in the soil that is entered by above and belowground plant residues. Overall, the global soil C reservoir with about 1550 Gt of organic carbon and 950 Gt of inorganic C (Lal, 2004) represents 80% of the earth's terrestrial C stock (IPCC, 2007). That is twice the amount of the atmospheric C pool and three times the quantity of the C pool stored in terrestrial plants. The net C balance of input (organic residues) and output (soil respiration) C fluxes as well as the ecoregion specific conditions determine the soil organic C (SOC) stock over time. As opposed

to temperate regions, there is an acceleration of human-induced SOC losses in the tropics due to higher soil temperature and moisture regimes. In a meta-analysis by Don *et al*. (2011) highest SOC losses in tropical regions were found for land-use changes from primary forest to agricultural land. 28% of SOC was lost after conversion to cropland, whereas lower losses (12%) were found for pasture establishment.

In particular, the interactions between plant and soil microorganisms are the main drivers of the C flux out of and into the soil (Craine *et al*., 1999). Previous studies investigated direct links between C flux and changes in the microbial function and structure (Allison *et al*., 2010; Singh *et al*., 2010). Complex interactions exist between plants, soil organisms, and geochemical constituents of soil, which play a key role in regulating soil C and nutrient cycling (Ehrenfeld *et al*., 2005; Swift *et al*., 1979) (see also Fig. 1.1). The largest global C transfer from terrestrial ecosystems to the atmosphere is the soil CO_2 flux through soil respiration (heterotrophic and autotrophic) that comprises about 80.4 ± 1.1 Gt C a^{-1} (Raich *et al*., 2002; Rodeghiero *et al*., 2009), whereas the estimated annual soil C storage capacity of atmospheric C can be 0.6 to 1.2 Gt C (Lal, 2004). Thus, even slight changes in soil C stocks due to enhanced soil respiration may cause major consequences for global C dynamics. In general, evergreen broad-leaved forests of the tropics and subtropics emit the highest annual soil CO_2 amounts (22.94 Gt C a^{-1} ≈30% of total) compared to any other vegetation type (Raich *et al*., 2002).

1.1.2 The role of soil microbes

Soil organisms comprise mega- and macro-fauna (e.g. mole, earthworms), meso- and micro-fauna (e.g. springtails, protozoa), and microflora (archaea, bacteria and fungi), the latter being the main drivers of soil organic matter (SOM) formation and dynamics. With its huge abundance, diversity and interaction, soil microbes play a main role in providing ecosystem services, such as the restoration, maintenance or improvement of soil fertility that humans require for agricultural production (Bardgett and Wardle, 2010; Kibblewhite *et al*., 2008; Mulder *et al*., 2011). In this context, soil fertility is defined as the capability of a soil to supply e.g. nutrients, water, aeration for plant growth to obtain a specific crop yield (Mengel *et al*., 1999).

Soil microbes are the greatest reservoir of nutrients compared to other living organisms (Whitman *et al*., 1998) that can be available for plants in the short-term. Additionally, soil microbes are important participants in many ecosystem processes, such as decomposition, C- and nutrient cycling or soil formation (Bardgett and Wardle, 2010). By producing extracellular enzymes, soil microbes catalyze the degradation of complex organic substances, in particular the breakdown of polymers into dissolved organic substances (Schimel and Bennett, 2004).

As reviewed elsewhere (Fierer *et al*., 2009; Wardle, 1998), the amount of microbes in the soil is highly variable across time and space and mostly associated with the amount of SOM. Whereas desert soils host about 43 g C m^{-2}, tropical forest soils can host more than 175 g C m^{-2}. Soil microbial properties, such as growth and metabolism can be significantly affected by the bioavailability and biodegradability of SOM (Marschner and Kalbitz, 2003). The biodegradability comprises the quantity and quality (ratios of C/N, cellulose to lignin, and lignin to N) of organic residues, whereas physico-chemical properties (e.g. soil texture, porosity, temperature, moisture, and pH) (Davidson *et al*., 2006; Paterson *et al*., 2009) as well as the potential for access (adhesion to mineral surfaces and/or occlusion of OM) describe its bioavailability.

The capability of a microbial community to mineralize macromolecular C compounds can differ depending on the functional traits of specific microbial groups (Waldrop *et al*., 2000). In general, functional traits (copiotrophic *vs.* oligotrophic) are not yet fully explored (De Deyn *et al*., 2008). However, it has been hypothesized that fungi (C/N about 10) have a higher efficiency to incorporate C into biomass than bacteria (C/N about 4) (Six *et al*., 2006). The dominance of a fungal community in soil is mainly associated with a low substrate quality leading to higher SOM contents since fungal metabolites are nutrient-poor and remain for longer time periods than bacterial ones (Bardgett *et al*., 2005).

In general, it is believed that energy/C availability is the major physiological limitation of soil microbes in most ecosystems. However, if the quantity of any essential nutrient of the soil microbes is low, it will induce stress and reduce microbial metabolism (Paul, 2007). In a wide range of tropical soils P availability is the major constraint of biological activity. P limitation to microbial processes was found in Oxisols of moist tropical forests in Costa Rica where low P availability limited SOM mineralization rates (Cleveland *et al*., 2002). It was assumed that this decrease in P mineralization rates is associated with a change in the microbial community structure (Townsend *et al*., 2002) leading to an amplified P limitation for plant growth in these soils. Microbial N limitations may occur in rather old or degraded tropical pastures where N is leached or stored in more recalcitrant OM of invaded plants. This process may primarily cause constraints on energy/C availability of soil microbes. Microbial N acquisition is of general importance since N is an important building block for protein synthesis and used for the production of extracellular enzymes involved in the OM decomposition (Sinsabaugh *et al*., 2005; Whitehead, 2000). Extracellular enzymes consist of high N contents (8-32% N). As a consequence, it is assumed that N addition to a microbial N-limited soil may lead to increased production of phosphatases that are able to decompose more recalcitrant OM (Waldrop and Firestone, 2004).

1.1.3 Plant-microbe interactions

Intensive interactions between plant and soil microbes exist that regulate ecosystem processes (Ehrenfeld *et al*., 2005). Especially the flow of C and nutrients into and out of the soil are regulated by plant-microbe interactions controlling the balance between primary production and decomposition (De Deyn *et al*., 2008). The capacity of C sequestration within ecosystems can be considerably influenced by plant-microbe interactions (De Deyn *et al*., 2008; Nielsen *et al*., 2011; Wolters *et al*., 2000), whereas these direct relationships can be mutualistic (e.g. N-fixing bacteria, mycorrhizal fungi) or antagonistic (pathogens, parasites) (Bardgett, 2011).

On the one hand, plant growth and plant community dynamics depend e.g. on the nutrient supply of soil decomposers (Bardgett, 2011). On the other hand, the resource availability for decomposer organisms is predominantly regulated by the quantity and quality of above- and belowground residue inputs by plants (Bardgett and Wardle, 2010; Dijkstra *et al*., 2006). Chemical composition of plant litter (e.g. C/N-, C/P-, N/P-ratio, and composition of functional polymers, such as lignin, tannins, starch, cellulose, hemicelluloses) and of root exudates determine the rate of OM decomposition, whereas soil C and nutrient resources mainly control litter quality (Chapin *et al*., 2002). Thus, the mineralization of OM and liberation of nutrients into the soil environment by heterotrophic soil microbes depend on plant traits (De Deyn *et al*., 2008) including plant productivity, litter N concentration and rhizodeposition (Dijkstra *et al*., 2006).

The SOM mineralization rate, mediated by soil microbes, can be substantially influenced by plant roots through the input of easily available substrates (root exudates) (Kuzyakov, 2002). This process may induce an acceleration or retardation of SOM mineralization in the short-term which is defined as a positive or negative priming effect (PE), respectively (Kuzyakov *et al*., 2000). Its magnitude in response of above- and belowground modifications determine gains or losses of SOM (determined as alterations in CO_2 efflux or N mineralization) in the soil system (Chapin III *et al*., 2009). Previous studies have shown that the occurrence of PEs can depend on several factors like quantity and quality of above- and belowground residue inputs, on fertilizer amendments, drying and rewetting cycles, mechanical disturbance of soil aggregates as well as on soil pH (Blagodatskaya and Kuzyakov, 2008; Fontaine *et al*., 2003; Kuzyakov *et al*., 2000). However, direction and magnitude as well as ecological significance of PEs in different ecosystems still have to be investigated, in particular with respect to land-use induced changes in SOM dynamics (Kuzyakov, 2010).

Land-use changes are often associated with alterations in the net primary productivity which can increase or decrease the C-input to ecosystems (Wardle *et al*., 2012). Land abandonment and ongoing succession is one example for functional shifts in the vegeta-

tion structure from fast-growing, short-statured plant species to slow-growing, long-lived ones. These alterations may reduce OM turnover rates and induce a shift in the microbial community structure. As a result, OM can accumulate aboveground (organic layer) and soil microorganisms with unique traits, which are able to facilitate specialized C cycling processes, may diminish or become less important. Others may invade the soil system fundamentally changing the C and nutrient cycling processes. However, it was also found that microbial communities could be resistant (no change), resilient (recover quickly) or functionally redundant to human-induced land-cover changes (Allison and Martiny, 2008; Nielsen *et al*., 2011; Rousk *et al*., 2009). Soil microorganisms with their high abundance, rapid growth rate and diversity are capable of adapting their functions to changed environmental conditions (Paterson *et al*., 2009) and assume functions of diminished microbes. Overall, functionally equal traits of soil microorganisms are not prevalent throughout the entire community and species-specific impacts on soil C and nutrient dynamics have to be taken into account.

In addition to the benefit of plant-microbe interactions, also competition for nutrients (e.g. N and P), especially in the rhizosphere, exists (Marschner *et al*., 2011). As reviewed by Kaye and Hart (1997), heterotrophic microbes, that exhibit rapid growth rates, can be a strong competitor for inorganic N compared to plants. However, this is only a short-term sink of nutrients in the soil, since the microbial-nutrient pool cycles faster than the plant-nutrient pool. For the re-mobilization of microbially assimilated nutrients different regulation mechanisms are present in the soil, such as drying and rewetting effects in the soil environment as well as predation on microbes by specific nematodes, protozoa, and microarthopodes with release of excess nutrients (Bardgett and Wardle, 2010). However, further investigations are needed to fully elucidate plant–microbial competitions.

1.1.4 Impact of soil environment on soil microbes

The soil environment that comprises soil texture and aggregates as well as the soil pH, soil temperature and moisture conditions (physicochemical properties) can be significantly changed by alterations in land-use, vegetation and climate. These soil environmental conditions influence the microbial substrate availability and are also important determinants of soil microbial amounts, eco-physiological status and community composition (Bååth and Anderson, 2003; Bardgett and Wardle, 2010; Fierer and Jackson, 2006; Lauber *et al*., 2008; Rousk *et al*., 2010a). In Costa Rica, the conversion of tropical forest to pasture caused severe changes in the soil environment of a nutrient-poor Oxisol. For example, pasture establishment increased bulk density and decreased pH value which caused a significant decline in the microbial biomass and activity (Cleveland *et al*., 2003). However, the authors found out the microbial response to pasture establishment to be more pronounced in Oxisols than in more fertile Mollisols.

Climate changes can lead to increases or decreases in soil temperature and moisture conditions (Singh *et al*., 2010). However, universal feedbacks of microbes, such as accelerated mineralization processes due to increased soil temperatures are still under debate since substrate availability can also be influenced by other factors affecting microbial decomposition (Davidson and Janssens, 2006; Kirschbaum, 2006). In contrast to regions with a pronounced seasonal climate, tropical wet regions (equatorial and mountain rainforests), as investigated in the present study, are characterized by a perhumid climate where monthly precipitation exceeds 100 mm and amplitudes of mean daily air temperatures are below 2°C throughout the year. There, the soil moisture regime does not change significantly and daily soil temperature amplitudes are higher than yearly ones (Cleveland *et al*., 2003). It is expected that soil microbes are adapted to and not limited by these prevailing soil temperature and moisture conditions and soil physicochemical properties may rather be the main trigger of soil microbial properties.

The H_3O^+ concentration of the soil solution is a further important determinant of soil microbial response. Especially the solubility and ionization of organic substances and metals in the soil solution as well as mineral weathering depends on soil pH. Different factors, such as inherent soil properties, concentration of FeS_2, litter quality, rhizodeposition, fertilization, liming, and acid rainfall can regulate soil acidity (Paul, 2007). Alterations in soil acidity can have important impacts on the microbial activity since OM availability can be increased or decreased. Furthermore, enhanced metal ion concentration (e.g. Al, Zn, Cu) due to decreased pH values can be toxic for microbes. On a continental scale, the diversity and richness of bacteria was lower in more acid than in neutral soils (Fierer and Jackson, 2006). Different microbial groups, such as bacteria or fungi can have distinct pH optima in soil (Fernandez-Calvino *et al*., 2011; Rousk *et al*., 2009). However, the causality among environmental factors is still uncertain, and investigations are needed to elucidate the main trigger controlling soil microbial responses in terms of land-use changes.

1.2 Pasture establishment in the tropics

In the tropics population growth, governmental policies, and poverty of smallholder farms are driving forces of continuously expanding pasture land at the expense of natural forest ('t Mannetje *et al*., 2008; de Koning *et al*., 1998). Since the 1960s the demand for milk and meat has doubled and tripled, respectively, in the developing countries (FAO, 2009). Especially in Latin America conversion of forest to extensive grazing land has increased markedly over the last decades (Wassenaar *et al*., 2007). In 2007 27% of the total Latin American and Caribbean land was used as pastures, whereas only 7% was used as arable land (FAO, 2009).

Pasture productivity is influenced by multiple factors, e. g. inherent soil fertility, climate, geomorphology, fire frequency, grass type, livestock density as well as form and load of fertilizer (Dias-Filho *et al*., 2001). A reduction in pasture productivity together with soil erosion, soil C loss and deteriorated water cycles are considerable environmental consequences of pasture degradation ('t Mannetje *et al*., 2008). Large parts of Latin American pastures are threatened by the loss of soil fertility (especially P, N) since soils are inherently poor in nutrients and mostly acidic (Montagnini, 2008). Additionally, the invasion of non-fodder plant species that compete with grasses for nutrients and light can be a further risk of pasture degradation. As a consequence of severe land degradation, the incomes of farmers decrease due to reduced milk or meat production and increased production costs. Thus, a sustainable pasture management is crucial to stabilize pasture systems and to avoid extensive land degradation. To conserve nature and to improve the environment in the tropical regions, rehabilitation/ restoration of degraded pastures to recover their productivity (Montagnini, 2008) as well as reforestation (Marin-Spiotta *et al*., 2009; Silver *et al*., 2004) are recommended and will be on focus in the future (Lal, 2003).

To successfully manage tropical pastures it is crucial to understand soil biogeochemical changes, their variability and their regulation mechanisms following deforestation (Neill *et al*., 1997b). As discussed in Section 1.1 land-use changes are associated with severe impacts on soil biogeochemical cycles (trace gas emissions, C and nutrient cycling, and hydrological cycle) which are mediated by soil microbes (Feigl *et al*., 2008; Lal, 2005). In general, soil pH value as well as base saturation increased after ash-input of burned forest biomass and pasture establishment (Krishnaswamy and Richter, 2002; Makeschin *et al*.,

2008; Veldkamp, 1994). This increased pH value at the pasture sites can persist over decades depending on their management. Krishnaswamy and Richter (2002) assumed that additional ash-input by frequent pasture fires as well as input of base-rich feces of livestock may have prevented soil acidification. Furthermore, tropical pasture soils had lower net nitrification rates than forest soils contributing to the maintenance of higher pH values in the soil solution (Reiners *et al*., 1994).

Several studies in Latin America investigated changes in soil microbial dynamics (Cleveland *et al*., 2003; Kaschuk *et al*., 2010) altering soil C storage as well as N transformations (Hughes *et al*., 2002; Neill *et al*., 1999; Rhoades and Coleman, 1999; Veldkamp *et al*., 1999) and P transformations (Friesen *et al*., 1997; Garcia-Montiel *et al*., 2000; Townsend *et al*., 2002) substantially. Different patterns of SOC storage were found after pasture establishment. Apart from increases in SOC stocks (de Moraes *et al*., 1996; Neill *et al*., 1997a) also decreases (Desjardins *et al*., 2004; Trumbore *et al*., 1995; Veldkamp, 1994) or no effects (Feigl *et al*., 1995a) were investigated. Overall, a recent meta-analysis in the tropics (Don *et al*., 2011) revealed that the conversion of primary forest to pasture caused a depletion of SOC stocks by about 12.6 Mg ha^{-1} (±3.0 SEM) with a prior forest SOC stock of 73 Mg ha^{-1} (93 studies, on average: 36 cm soil depth; 25 years after land-use change). SOC losses enhanced with increasing temperature and precipitation. However, since soil mineralogy and pasture age along with tropical pasture management may also be important factors for soil C storage and turnover, no general conclusions about the impact on soil C-sequestration can be drawn (Davidson *et al*., 1995; Fearnside and Barbosa, 1998; Powers and Veldkamp, 2005).

Furthermore, the impact of pasture establishment on function and structure of soil microorganism can vary widely across soil type, climate and pasture management (Cleveland *et al*., 2003; de Moraes *et al*., 1996). In the Amazon Basin net N as well as P mineralization rates were found to be increased in the short-term, immediately after forest conversion, whereas in the long-term rates declined markedly with pasture age as compared to primary forest (Garcia-Montiel *et al*., 2000; Hughes *et al*., 2002; Neill *et al*., 1999; Townsend *et al*., 2002). The rapid decline in P availability was mostly associated with transformations from easily available P forms to less soluble ones (organic P, occluded P) (Garcia-Montiel *et al*., 2000; Hamer *et al*., 2012a). Soil N dynamics of pasture soils can also be influenced by grass properties. For a tropical lower montane forest region Rhoades and Coleman (1999) detected a higher potential of N immobilization at pastures with a deep-rooted grass (*S. sphacelata*) compared to mixed grass species. These changes in nutrient cycling can also be related to changes in the whole microbial community structure. In Hawaii, bacterial communities changed significantly after pasture establishment which was mainly related to altered substrate availability and increased pH value (Nüsslein and Tiedje, 1999).

1.3 Research area

The research area is situated in the mountain rainforest region of southern Ecuador, on the eastern slopes of the eastern Andean cordillera (Cordillera Real), in the valley of Rio San Francisco (Fig. 1.2). An extraordinary diversity of vascular plants (Barthlott *et al*., 1996; Richter *et al*., 2009) and birds (Orme *et al*., 2005) qualify this region as one of 25 biodiversity hotspots of the world, facing a high risk of elimination (Myers *et al*., 2000).

In general, Ecuador exhibits by far the highest annual deforestation rate in South America (Mosandl *et al*., 2008) reducing the country's forest cover by 1.8% per year (2005–2010) (FAO, 2010). Poverty and an annual population increase of 1.4% (Pan *et al*., 2007; UN, 2010) are major drivers for these alarming deforestation rates. Hence, even in the San Francisco valley, large parts of the mountain rainforest, especially along the road between the two provincial capitals Loja and Zamora, have been removed to gain pasture land. There, the economy of the farmers is primarily based on cattle ranching for milk production (Pohle and Gerique, 2006) since an alternative agricultural use is unfavorable due to steep slopes and high precipitation.

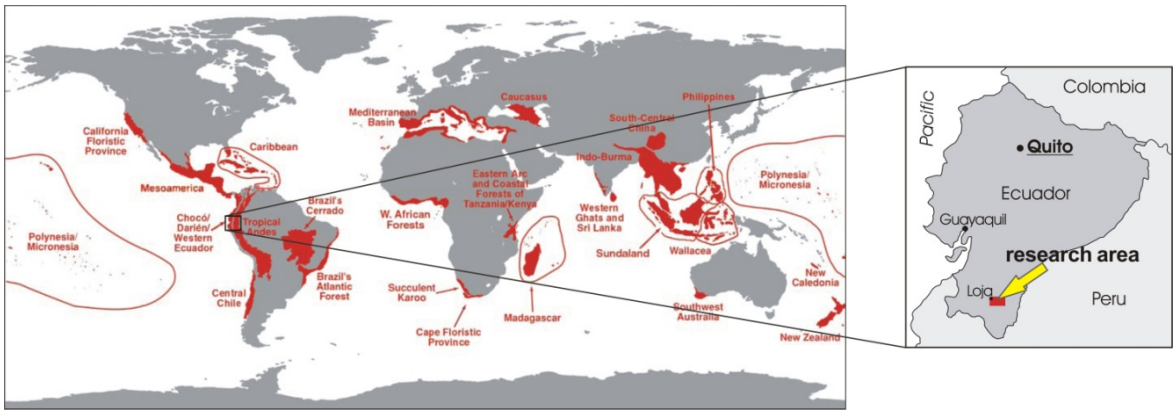


Figure 1.2: Left: global biodiversity hotspots (Myers *et al*., 2000). Right: location of the research area within the hotspot of "Tropical Andes.

Commonly used pasture grasses are *Setaria sphacelata* (Schumach.) Stapf & C.E. Hubb., *Melinis minutiflora* P. Beauv, and *Holcus lanatus* L. (Gawlik, 2010; Gerique, 2010). Especially the tropical C_4-grass *Setaria sphacelata*, originating from Africa (Hacker and Jones, 1969), is widely used in the San Francisco valley. This grass species was introduced into the region in the early 1950s (Gerique, 2010). *Setaria* is characterized by a high resistance to uncontrolled human-induced fires and is best suited to the prevailing climatic conditions (sum of precipitations >750 mm a^{-1}) (Dwivedi and Kumar, 1999). Furthermore, compared to traditional, mixed grass communities, *Setaria* grows rapidly and has a higher resistance to weed invasion, attributable to its dense fine-root system (Rhoades *et al*., 2000). However, unfortunately, these pastures also become progressively less productive due to in-

appropriate pasture management, such as recurrent burning, and especially due to the invasion (Dias-Filho *et al*., 2001) of the vigorously growing southern bracken fern (*Pteridium arachnoideum* (Kaulf.) Maxon and *caudatum* (L.) Maxon). When the pasture grasses are outcompeted by the bracken, the farmers are forced to abandon these areas (Hartig and Beck, 2003; Roos *et al*., 2010a) and to convert further natural forest for maintenance of their livestock. To prevent pasture degradation, and thus area expansion, a sustainable land management is needed which can only be achieved by combining social-economic principles with environmental concerns (de Koning *et al*., 1999; Smyth and Dumanski, 1995).

The present study was realized within the multidisciplinary DFG (Deutsche Forschungsgemeinschaft) research unit RU816 "Biodiversity and Sustainable Management of a Megadiverse Mountain Ecosystem in South Ecuador" (www.tropicalmountainforest.org), launched in 2007. One objective of the investigations is to quantify and/or estimate the impact of the encroachment and intensification of land-use on ecosystem functioning/ services in the research area. The logistic center of the RU816 is the research station Estación Científica San Francisco (ECSF) which is located in the San Francisco valley at 1,860 m asl (3°58'18'' S, 79°4'45'' W) (Fig. 1.3). The ECSF is an ideal starting point for investigations along a land-use gradient. Natural forest of the Reserva Biológica San Francisco (RBSF altitudinal gradient: 1,600–2,930 m asl), that directly border the protected area of the Podocarpus National Park, can be compared with patches of active and abandoned pastures on the opposite, south-facing slopes. Especially on these slopes the expansion of deforested land is high, comprising a deforestation rate of 0.6 to 0.9% annually (Goerner *et al*., 2007).

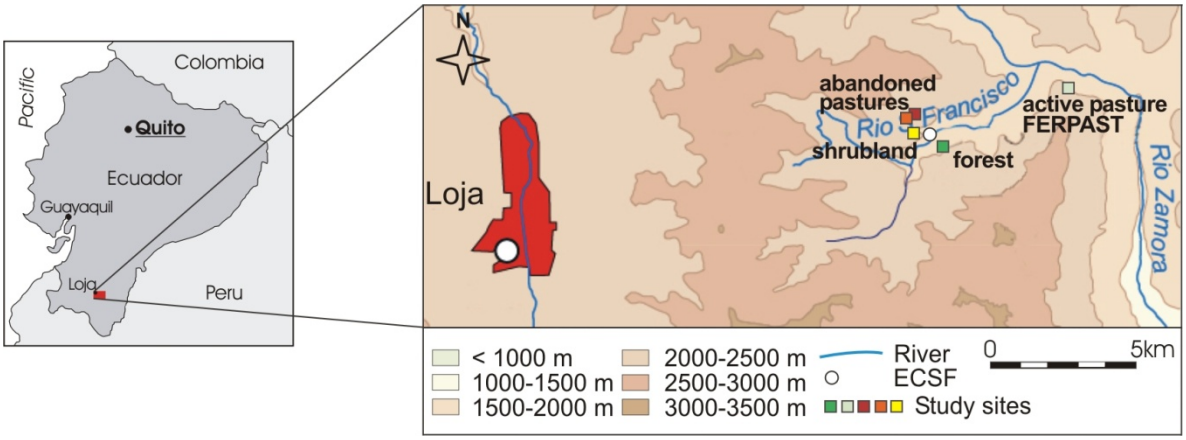


Figure 1.3: Overview of the geographical position of the study sites. Modified map according to Richter (2003).

The climate of the research area is perhumid with a less humid period from September to December. However, since mean monthly rainfall never falls below 100 mm, no pronounced seasonality exist (Bendix *et al*., 2006). Precipitation rates show a strong altitudinal gradient (Fabian *et al*., 2005). From the ECSF (1,860) to the crest zone (2,930 m asl), mean annual precipitation and cloud/ fog water deposition (including horizontal rainfall) nearly triple, reaching tremendous water intakes of 6,090 mm (Bendix *et al*., 2008), whereas mean annual air temperatures decrease from 15.3 to 9.5°C (Bendix *et al*., 2006).

Evergreen lower and upper mountain rainforests cover the steep slopes of the Reserva Biológica San Francisco. The crest areas are covered by altotropical evergreen scrub páramo (grass- and shrubland) (Richter, 2003). These forests are characterized by a high species richness of shrubs, herbs, epiphytes as well as of trees where Melastomataceae, Lauraceae, Rubiaceae, and Euphorbiaceae are dominant plant families (Homeier and Werner, 2008; Moser, 2008).

In general, extremely steep slopes, and deeply incised valleys, as the Rio San Francisco valley, characterize the relief of the eastern Andean cordillera. Frequently occurring natural landslides are a typical feature of the landscape due to steepness, geomorphologic instability, high precipitation and sometimes due to earthquakes (Bussmann *et al*., 2008). These natural dynamics of the ecosystem are expected to contribute to the mega-diverse biodiversity hotspot of vascular plants, forming patches of temporarily open habitats in different stages of succession (Richter *et al*., 2009). Thus, natural land sliding facilitates the maintenance and development of high plant species richness (Bussmann *et al*., 2008; Muenchow *et al*., 2012; Wilcke *et al*., 2003).

Geologically, the research area belongs to the Paleozoic metamorphic belt (Chiguinda Unit of Zamora Series) (Litherland *et al*., 1994) comprising a great variety of weakly metamorphosed bedrocks, such as metasandstones, metasiltstones, clayschists, and phyllites with some quartz veins (Makeschin *et al*., 2008). The substrate for pedogenesis is considered to be low in nutrients. Furthermore, pedogenetic processes are markedly affected by (i) the altitudinal gradient where the influence of hydromorphic processes increases with increasing altitude (Ließ *et al*., 2009), (ii) the relief inducing different hydrological conditions between ridges and side valley creeks (Wilcke *et al*., 2008a), (iii) the occurrence of natural as well as anthropogenic landslides (along roads) forming different layers of pedogenetic substrate (Bahr, 2007; Wilcke *et al*., 2003), (iv) drawbacks of the mega-diverse vegetation e.g. through influencing the turnover rates of litter (Ließ *et al*., 2009; Wilcke *et al*., 2008b), and by (v) land-use change e.g. through the loss of the organic layer and especially of nutrients after slash and burn of natural forest (Hamer *et al*., 2012a; Makeschin *et al*., 2008). According to the WRB (FAO, 2006) Histosols, Regosols, Cambisols and Stagnosols are the main soil types between 1,800 and 2,300 m asl (Bahr, 2007; Schrumpf, 2001). In the natural forest the soils are characterized by a thick organic layer of up to 50 cm (Wilcke *et al*.,

2008b) comprising the majority of the roots and a large fine-root system (Röderstein *et al*., 2005; Soethe *et al*., 2006). About 40% of the organic carbon stored in the uppermost 30 cm of the soil is located in the organic layer and top 10 cm of the mineral soil. Additionally, most of the plant available nutrients are stored in the organic layer. Investigations of the mineralization processes emphasized the importance of the organic layer for nutrient turnover in this ecosystem, generally being nutrient-limited due to e.g. low litter quality and high precipitation (Iost, 2007; Wilcke *et al*., 2002). The forest mineral soil is strongly acidic (pH ≤ 4.0), has a low cation exchange capacity (CEC), low total P contents (Makeschin *et al*., 2008) and a loamy soil texture (Ah-horizon).

2 Objectives and research questions

Although several studies have shown that land-use changes are associated with alterations in above- and belowground OM inputs to soils, different abiotic and biotic soil conditions of the respective study area can have various effects on SOM dynamics. This fact makes predictions of soil ecosystem responses to land-use changes, such as SOC losses or nutrient supply for plant growth, difficult.

In the present study, specific attention was paid to determine the impact of forest-to-pasture conversion and of pasture abandonment on SOM dynamics with a special focus on soil microbial responses (function and structure) (Section 2.1). Additionally, a pasture fertilization experiment with urea and/or rock phosphate was conducted with regard to possible beneficial effects on soil microbial properties and pasture productivity (Section 2.2).

2.1 Land-use change

In the area of study, deforestation rates of the endangered mountain rainforest are still high and large parts of the established pasture land become progressively less productive, leading to huge areas of abandoned land overgrown by bracken. Examining the processes behind pasture degradation will help to find strategies for its prevention or for pasture regeneration of abandoned areas. Along a land-use gradient, investigations of the complex network of feedbacks between soil microbes and their abiotic environment are needed to gain a better understanding of the overall impacts of forest-to-pasture conversion and pasture abandonment on soil C and nutrient dynamics. In previous investigations along the land-use gradient (*natural forest – active pasture – abandoned pasture – shrubland*) it was established that pasture establishment was associated with a decreased soil C/N ratio and with an increased pH value that persisted over decades in the topsoil (Makeschin *et al*. 2008; Hamer *et al*. 2012a). It was hypothesized that changed soil conditions at the newly established pasture are beneficial for microbial metabolism and growth. Long-term pasture use and the infestation of pastures by bracken seemed to decrease soil quality and thus caused deterioration of soil fertility.

The main objectives of the present work were to determine:

(i) whether the expected increase in the bioavailability and biodegradability of SOM to soil microbes after pasture establishment might be beneficial for microbial function in newly established pastures, and

(ii) whether bracken-invasion and pasture abandonment might revert such favorable effects due to alterations in litter quality.

Following research questions concerning land-use changes guided the thesis:

To what extent is the C transfer from the soil to the atmosphere influenced by pasture establishment and abandonment? [see Potthast *et al*. (2011) in Section 4.1]

- Is the in situ soil CO_2 flux higher or lower at the pasture sites compared to the natural forest?

What impact has the planting of the pasture grass (C_4) as well as the bracken-invasion (C_3) on the SOM pool in the topsoil? [see Potthast *et al*. (2010; 2011) in Section 4.3 and 4.1]

- Which SOC source is preferentially mineralized by the soil microbes at the pasture site – the "old" C derived from the former forest (C_3-plants) or the "new" C derived from the pasture grass (C_4-plant) and which C pool dominates in the active and abandoned pasture soils? [Section 4.3]

What are the main aspects and drivers of soil fertility loss during pasture use in the study area? [Section 4.3; 4.1]

- How far are soil C and N availability as well as soil pH affected by pasture establishment and abandonment?

- To what extent does especially the invasion of bracken influence these soil properties?

How do microbial function and structure respond to expected changes in soil substrate availability and in environmental conditions along the land-use gradient? [Section 4.3; 4.1]

- Are soil microbes energy and/ or nutrient-limited?

Current data of microbial properties of the *abandoned pasture low pH* site were taken for comparison with all other investigated study sites (*natural forest*, *active pasture*, *abandoned pasture*, and *shrubland*) to examine the question:

- Is the soil microbial function and structure affected by increased soil acidity after long-term abandonment of pastures? [Section 4.2]

2.2 Pasture management

Based on the reasons for soil fertility loss during pasture use and abandonment, it was hypothesized that in the study area, where farmers do not use fertilizer, soil microbes as well as pasture productivity are limited by N and/or P on active pastures. It was expected that a higher biomass production of the *Setaria*-grass through fertilization could help to sustain its competitiveness against bracken-invasion. Additionally, it was assumed that this could prevent further pasture degradation through the maintenance or even through the increase of the available soil nutrient pool, which would be a first step towards a sustainable pasture management.

Thus, the specific objectives were to examine:

(i) whether the fertilization with urea and/or rock phosphate would affect the soil microbial structure and function,

(ii) whether the quantity and/or quality of the pasture grass would be influenced by fertilizer application, and

(iii) whether fertilization might alter soil respiration rates, changing the net C balance of the pasture ecosystem. [see Hamer *et al*. (2009), Potthast *et al*. (2012) in Section 4.4]

More detailed objectives are given in the introduction of the respective publications (Section 4).

3 Methodology

3.1 Study sites

3.1.1 Land-use gradient

In 2007, sites along a land-use gradient were selected in a circular of 5 km around the ECSF at about 2,000 m asl: *natural forest* – *active pasture* – *abandoned pastures* – *shrubland* (Figure 1.3 and 3.1). Main soil type at all sites is a Cambisol (FAO, 2006). Further characteristics of the Cambisols and of the main plant species of the different sites as well as their exact location are presented in Table 3.1. The Cambisol of the *natural forest* soil differs from both pasture sites by having a thick organic layer (O_i and O_eO_a) of about 11 cm (prefix qualifier "Folic") and some parts of reducing conditions between 50 and 100 cm from the mineral soil surface (prefix qualifier "Endogleyic"). The soil texture to 20 cm soil depth of all sites is similar with about 29% of sand and 39% of silt. At each land-use site six replicate plots (25 m² each) were randomly selected.

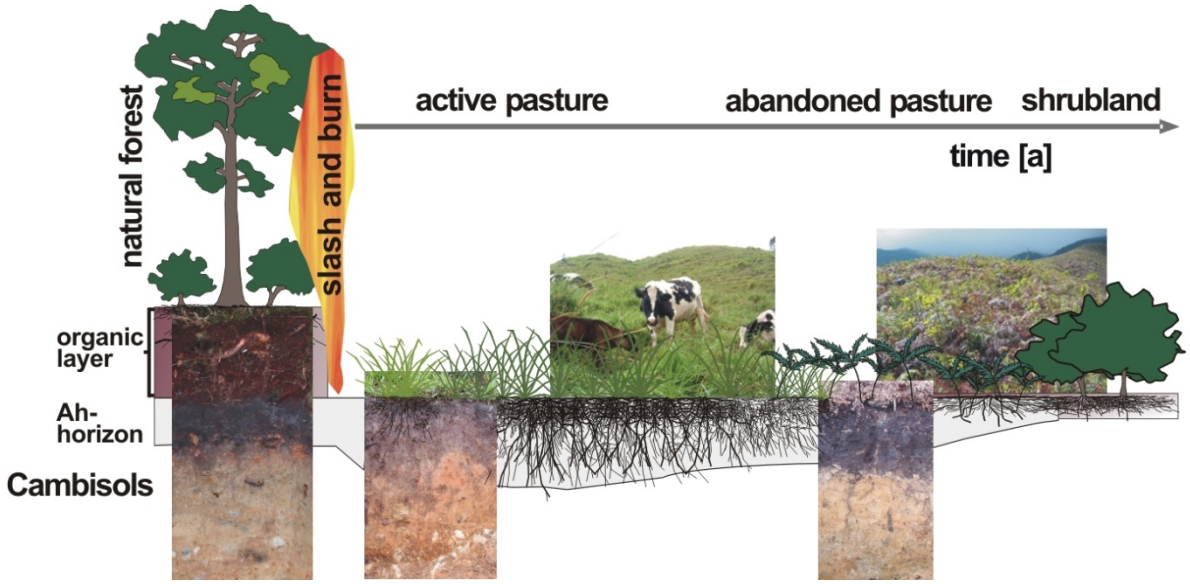


Figure 3.1: Scheme of the land-use gradient (*natural forest–active pasture–abandoned pasture*).

The *natural forest* site is a permanent study site (0.25 ha) selected by researchers of the previous research unit RU402 in the year 2000. Plenty investigations of different disciplines have been carried out, comprising determinations of the soil fauna (Krashevska et

al., 2008), of the structure and function of root systems (Soethe, 2006), and measurements of soil respiration (Iost *et al*., 2008). The selected pasture site was established by slash and burn 17 years ago, and *Setaria sphacelata* grows there in monocultures. Since then, the land has been extensively grazed by dairy cattle with a livestock density of one cow per hectare. Hereafter, this site is referred to as *active pasture*. Two adjacent abandoned pasture sites were selected for the present study (Fig. 1.3, Table 3.1). Both sites were former *Setaria*-dominated pastures and have been overgrown by bracken since the abandonment about ten years ago. These sites are mainly distinct from each other in their soil pH. The site with the higher pH(H_2O) value (5.2 in 0–5 cm) was referred to as *abandoned pasture* and the other as *abandoned pasture low pH* (4.1 in 0–5 cm). Soil samples of the latter site were used for the lab experiment of Potthast *et al*. (2010) (Section 4.3) and for discussions. The *shrubland* site was abandoned about 20 years ago and is dominated by successional bush vegetation (variety of herbs and shrubs, see Table 3.1). During succession an organic layer with a mean thickness of 8.3 cm has developed.

Table 3.1: General characteristics of the study sites along the land-use gradient.

	Elevation [m asl]	Coordinates	Soil type (WRB 2006)	Vegetation
natural forest	1,890	03°58´35´´S 79°04´65´´W	Folic Endogleyic Cambisol (Alumic, Humic, Dystric, Siltic)	Old-growth, evergreen lower montane forest with high species diversity: *Graffenrieda emarginata* and *Miconia* (Melastomataceae, 31%)*, *Ocotea* (Lauraceae, 13%)*, *Alchornia* (Euphorbiaceae)*, *Palicourea* (Rubiaceae)*, *Clethra* (Clethraceae)*
active pasture/ FERPAST	1,930	03°57´26´´S 79°02´19´´W	Haplic Cambisol (Humic, Siltic)	*Setaria sphacelata* (>99%)
abandoned pasture	2,100	03°57´51´´S 79°04´37´´W	Haplic Cambisol (Humic, Siltic)	*Pteridium arachnoideum* (approx. 85%) *Setaria sphacelata* (approx. 15%)
abandoned pasture low pH	2,135	03°57´52´´S 79°04´39´´W	Mollic Cambic Ultisol (Humic, Siltic)	*Pteridium arachnoideum* (approx. 95%) *Setaria sphacelata* (approx. 10%)
***shrubland* (succession)**	2,150	03°58´30´´S 79°05´19´´W	Folic Cambisol (Alumic, Humic, Dystric, Siltic)	*Pteridium arachnoideum* (approx. 50%) *Baccharis Latifolia* and *Ageratina dendroides* (Asteraceae)** *Monochaetum lineatum* (Melastomataceae)**

*Moser (2008); **Hartig and Beck (2003)

3.1.2 Pasture Fertilization Experiment (FERPAST)

In 2008, a pasture fertilization experiment (FERPAST) was set up at the 17-year-old active pasture site, which is part of the above described land-use gradient. The FERPAST experiment investigated the impact of nutrient addition on soil biochemical properties, on grass yield, and fodder quality. No fertilizer had been used at this site prior to the study. For the

fertilization experiment organic N-fertilizer (urea) and inorganic P-fertilizer (rock phosphate) was chosen. In a fenced area (0.5 ha), six replicate plots (25 m² each) of each treatment - **X** (control), **N** (urea), **P** (rock phosphate) and **NP** (combination of both fertilizers) - were randomly arranged as displayed in Figure 3.2. Moderate rates of 50 kg N ha^{-1} a^{-1} and 10 kg P ha^{-1} a^{-1} were used and evenly split into three applications per year. Grass biomass yield has been measured every 2 to 3 months. Further details of the FERPAST experiment are described in Potthast *et al*. (2012) (see Section 4.4).

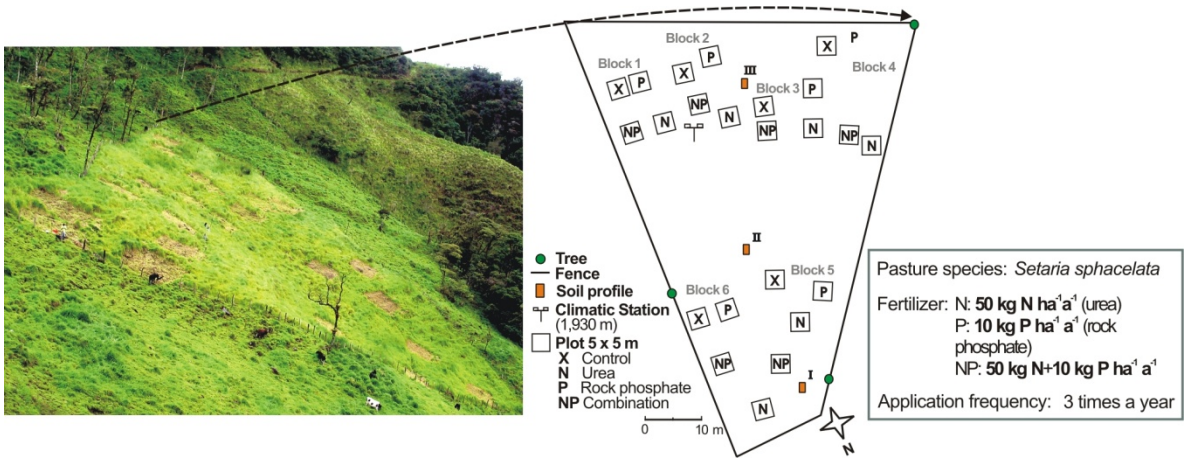


Figure 3.2: Scheme of the experimental design of FERPAST (Potthast *et al*., 2012).

3.2 General analyses

The following section gives an overview of the applied methods including laboratory analyses as well as in situ measurements at the study sites along the land-use gradient and upon fertilizer treatments (FERPAST). Besides the analyses of soil biogeochemical properties of each study site, leaves and roots of grass and bracken were analyzed for chemical characteristics.

Soil samples were taken on each of the six replicate plots (25 m²) with a soil corer (6 cm diameter, 5–10 cores per plot) and split into 0–5, 5–10 and 10–20 cm deep sections. One composite sample was prepared by deep section. Additionally, the organic layer of the *forest* and *shrubland* site was sampled and divided into Oi- and OeOa-horizons. In the laboratory, soil samples were analyzed for geochemical properties (pH, total C and N, total elements, DOC, TDN, PO4-P, CEC, δ13C) and in particular for microbial properties including the microbial amount of C (MBC), the amount of N and P incorporated (MBN, MBP), the activity (C and net N mineralization, gross N mineralization, and gross NH_4 consumption) and the community structure (PLFA-analysis). Samples of grass (*Setaria*) and bracken leaves and roots were analyzed for total C and N, total elements and lignin content. More

information on the applied methods is given in Table 3.2 and comprehensive descriptions are provided in the respective publications (Section 4).

Table 3.2: Analytical methods used to determine soil biogeochemical variables, chemical characteristics of plants and roots as well as function and structure of soil microbes.

Laboratory	Material and Method
pH	(H_2O) mineral soil:solution 1:2.5 and organic layer 1:10
total C, TN (soil, plants)	CNS-Analyzer (vario EL III/elementar, Heraeus, Hanau, Germany)
DOC, TDN	0.1 M KCl; multi-NC-analyzer for liquids (Analytik Jena, Germany)
inorganic P (PO_4-P)	0.03 M NH_4F + 0.025 M HCl (Bray I solution); continuous flow auto analyzer (Skalar Analytik GmbH, Erkelenz, Germany)
CEC	0.5 M NH_4Cl; ICP-OES (CIROS, Spectro Kleve, Germany)
total amounts of elements (soil)	HNO_3, HF, $HClO_4$; ICP-OES (CIROS, Spectro, Kleve, Germany)
total amounts of elements (plant shoots and roots)	HNO_3; ICP-OES (CIROS, Spectro, Kleve, Germany)
$\delta^{13}C$, $\delta^{13}CO_2$-C	EA-IRMS (Delta 2, Carlo Erba and Finnigan, Bremen, Germany)
^{14}C, $^{14}CO_2$-C	liquid scintillation counting (Beckmann LS 6000 TA, Fullerton, USA)
lignin	Klason-lignin
microbial biomass C, N,	0.5 M K_2SO_4; CFE-method; multi-NC-analyzer for liquids (Analytik Jena, Germany)
microbial biomass P	0.03 M NH_4F + 0.025 HCl; CFE-method; continuous flow auto analyzer (Skalar Analytik GmbH, Erkelenz, Germany)
C mineralization (1 to 14d)	0.05 M NaOH
net N mineralization (1d,14d) (NH_4-N, NO_3-N)	0.1 M KCl; continuous flow auto analyzer (Skalar Analytik GmbH, Erkelenz, Germany)
gross N mineralization **gross NH_4 consumption**	^{15}N-pool-dilution technique EA-IRMS (Delta 2, Carlo Erba and Finnigan, Bremen, Germany)
PLFA-analysis	GC-FID (GC 2010, Shimadzu, Japan)

3.2.1 Laboratory experiments

Two short-term incubation experiments (28 days) were carried out to examine the impact of (1) different litter quality (grass versus bracken litter) and (2) urea addition on biochemical properties of active and abandoned pasture soils. Both experiments focused in particular on the effect on C and N mineralization processes and on microbial community structure (PLFA-analysis).

(1) The first incubation experiment comprised non-amended microcosms of soil (*active* and *abandoned pasture low pH*, 0–5 cm) and litter (grass and bracken), used as control, as well as of soil microcosms amended with litter. For the latter, litters of grass (C_4) and bracken (C_3) were incorporated into field fresh soil samples of their corresponding origin sites and vice versa. During incubation, mineralization processes as well as microbial properties of the microcosms were investigated (microbial amount, activity, community struc-

ture). Since stable carbon isotopic signatures differ between grass and bracken litter, periodical $\delta^{13}CO_2$-C measurements were used to determine the C source mineralized by soil microbes (litter-C vs SOC). Further details about this experiment can be found in Potthast *et al*. (2010) (Section 4.3).

(2) The second incubation experiment comprised samples of *active* and *abandoned pasture* soil (0–5, 5–10 cm) that were either amended with ^{14}C- or ^{15}N-labeled urea. The isotopic labeling was applied to track the fate of ^{14}C into the microbial biomass pool and/or into CO_2, and that of ^{15}N into the microbial biomass and/or inorganic N pool (extracted by KCl). Equivalent amounts of urea were added as for the experimental site (FERPAST). Further information about the experiment can be found in Hamer *et al*. (2009) (Section 4.4).

3.2.2 In situ measurements

Weekly soil respiration measurements have been carried out over two years on active and abandoned pasture sites and on plots upon fertilizer treatment (Fig. 3.3a) to investigate the impact of bracken-invasion and fertilization on CO_2-C effluxes (see Potthast *et al*. (2011) in Section 4.1). Short-term influences of pasture fertilization on soil respiration rates were determined by measurements carried out after 1 hour, 1, 3, 5, 12, and 20 days of fertilization, respectively (see Potthast *et al*. (2012) in Section 4.4). Furthermore, a litterbag experiment (17 month) with grass (Fig. 3.3b) and bracken leaves was conducted, on the respective site of origin, to investigate the rate of litter decay (Potthast *et al*., 2011).

Figure 3.3: (a) Measurement of soil respiration and fertilization of collars and (b) litterbags of grass leaves at the *active pasture* site (FERPAST).

Each in situ measurement was compared to results determined by Iost *et al*. (2007) in a previous study at the *natural forest* site. There, the identical infrared gas analyzer for determination of soil respiration rates and the same litterbag equipment was used. Additional information about the field measurements are given in Table 3.3.

Table 3.3: In situ measurements used to determine soil respiration and grass and bracken litter decay.

In situ	Material and Method
soil respiration	infrared gas analyzer (IRGA, EGM 4, PP-Systems, UK)
litter decay	litterbag-experiment; 60 litterbags of grass and bracken leaves, respectively collection after 1, 2, 3, 10, 17 months for grass and after 1, 2, 3, 4, 8, 17 months for bracken

3.2.3 Statistics

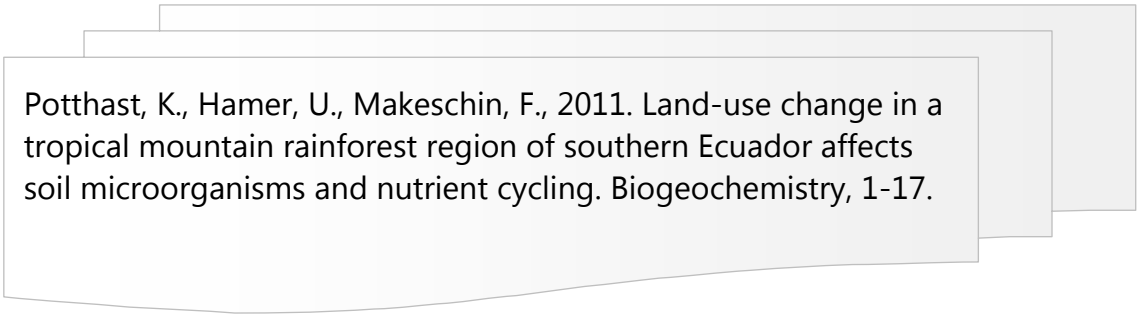
In the respective publications of the result section 4 the applied statistics are explained. For the evaluation of the impact of decreased pH value and ongoing succession on soil microbial properties (Section 4.2), a multivariate linear regression analysis and a redundancy analysis was applied. The number of variables (*n*) used for the analyses differed among sites since e.g. *active* and *abandoned pasture* sites were sampled several times. Prior to both analyses, datasets were checked for normality, and, if necessary, variables were square-rooted or log-transformed.

To examine correlations between the soil microbial biomass (MBC as response variable) and soil geochemical variables of all study sites along the land-use gradient (*natural forest, active, abandoned pasture, abandoned pasture low pH, shrubland*) multivariate linear regressions were used. The collinearity (tolerance) was checked for all variables, and redundant variables were stepwise removed from the model. The adjusted r^2 (r_{adj}^2) was used to elucidate the relationships and the variance partitioning according to Legendre and Legendre (1998) and to examine the respective pure effects of the single variables.

To elucidate the relationship among the microbial community structure along the land-use gradient (*natural forest, active, abandoned pasture and abandoned pasture low pH*) and respective soil biogeochemical variables (included as environmental variables) in 0–5 cm, a redundancy analysis (RDA) was applied. The RDA was conducted with Canoco 4.5 for Windows (ter Braak and Smilauer, 2002) where 28 identified PLFAs (mol%) and significant biogeochemical parameters (selected by Monte Carlo Permutation test, 499 permutations, $p<0.05$) were used for linear combination. For detailed description of the applied RDA method see Potthast *et al*. (2011) in Section 4.1.

4 Results

4.1 Soil C and nutrient dynamics along a land-use gradient



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4.2 Impact of pH and ongoing succession on microbial function and structure

When comparing biochemical soil properties along the extended land-use gradient it is clear that significantly higher values of available C and nutrients were found at the *natural forest* site (Table 4.1). Nevertheless, highest total N and P contents as well as amounts of microbial biomass C and N were detected at the *active pasture* site (Table 4.1, Fig. 4.1). It was shown that an increase of microbial biomass by a factor of three after pasture establishment was accompanied by a five-fold decrease after abandonment. During succession the microbial biomass increased again to forest levels (Fig. 4.1).

Table 4.1: Biochemical soil properties along the extended land-use gradient (0–5 cm, mean, SE). Significant differences between sites are indicated by different letters (Tukey test, p<0.05).

	n	SOC	TN	TP	MBN	DOC	DON	NH_4-N	NO_3-N
		--------- [%] ---------		---------- [mg kg^{-1}] ----------					
natural forest	*9*	8.5 (0.7)^{abc}	0.5 (<0.1)^{b}	367 (19)^{ab}	212 (18)^{a}	112 (17)^{c}	20 (5.6)^{b}	36 (7.0)^{b}	42 (6.1)^{b}
active pasture (X) FERPAST	*29*	10.3 (0.4)^{b}	0.8 (<0.1)^{c}	1143 (36)^{c}	596 (26)^{b}	68 (4)^{b}	8 (0.4)^{a}	5 (0.5)^{a}	1 (0.4)^{a}
abandoned pasture	*13*	7.9 (0.4)^{ac}	0.5 (<0.1)^{ab}	605 (76)^{b}	130 (15)^{a}	37 (4)^{a}	5 (0.6)^{a}	2 (0.6)^{a}	11 (4.2)^{a}
abandoned pasture low pH	*6*	7.3 (0.2)^{ab}	0.3 (<0.1)^{a}	204 (14)^{a}	98 (5)^{a}	45 (4)^{ab}	8 (3.5)^{ab}	8 (1.7)^{a}	1 (0.1)^{a}
shrubland (succession)	*5*	10.6 (0.8)^{bc}	0.4 (<0.1)^{ab}	n.d.	163 (12)^{a}	44 (5)^{ab}	4 (1.0)^{a}	1 (0.3)^{a}	0.2 (0.04)^{a}

n.d.=not determined

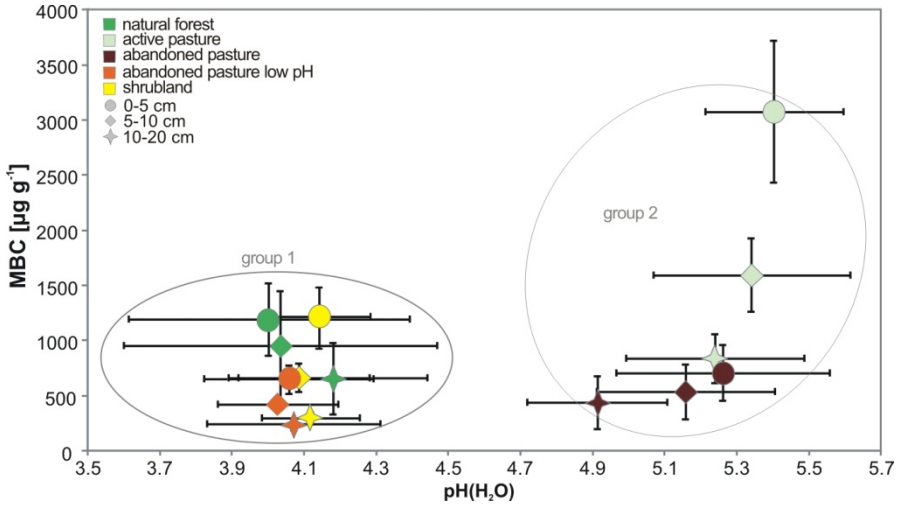


Figure 4.1: Comparison of the amount of microbial biomass C and respective pH(H_2O) of 0–5, 5–10, and 10–20 cm along the land-use gradient (mean±SD).

To determine whether the microbial biomass was directly influenced by soil pH, the amounts of MBC and respective pH values of all investigated sites were related to each other. As shown in Figure 4.1, the pH discriminated the dataset into two groups of sites. Group 1 (*abandoned pasture low pH*, *shrubland*, and *natural forest* referred to as G1) showed a mean pH range between 4.0–4.2 whereas the mean pH of group 2 (*abandoned* and *active pasture* referred to as G2) ranged between 4.9 and 5.4. Despite a one unit higher pH value at the *abandoned pasture* of G2, the microbial biomass of this site resembled the amounts found for G1. Thus, the pH value seemed not to be the main driver of the soil microbial amount. Multiple regression analysis of soil properties (SOC, TN, DOC, DON, TDN) in 0–5 cm soil depth with MBC of all sites revealed that 80% of the variance (r_{adj}^2=0.80) could be explained by the total nitrogen content being positively correlated.

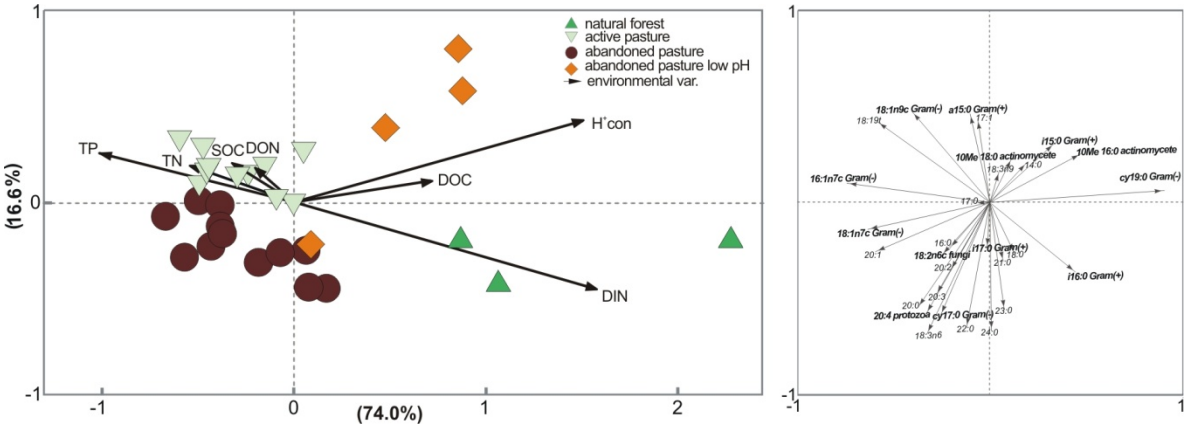


Figure 4.2: Ordination biplot (left) and corresponding loading plot (right) of a redundancy analysis (RDA) of the soil microbial community structure assessed with phospholipid fatty acid analysis [PLFA in mol%] and with biogeochemical variables (H_3O^+-concentration (H^+con), dissolved organic carbon (DOC), dissolved organic nitrogen (DON), dissolved inorganic nitrogen (DIN), soil organic carbon (SOC), total nitrogen (TN), total phosphorus (TP)) at 0–5 cm soil depth. The biplot shows the separation along the first and second axis of *natural forest*, *active pasture*, *abandoned pasture* and of *abandoned pasture low pH*.

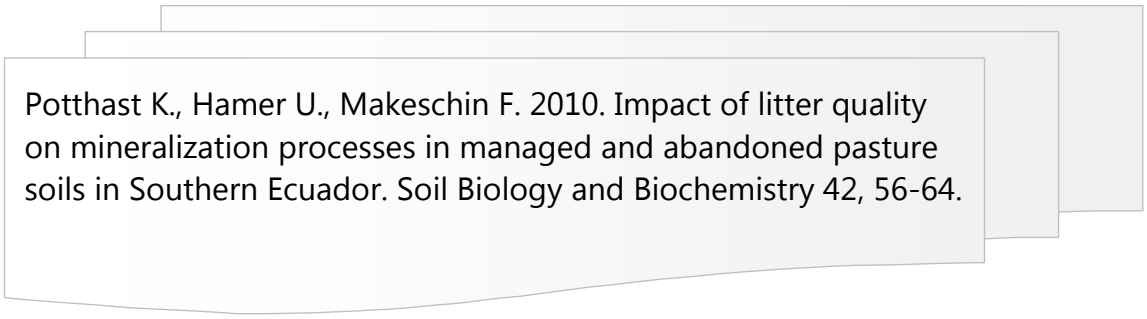
Along the land-use gradient the microbial community composition was determined in 0–5 cm soil depth except for *shrubland*. Results of the RDA revealed that *active* and *abandoned pasture* site plotted to the left along the first RDA axis displaying a lower distance to each other than to the *abandoned pasture low pH* and *natural forest* sites (Fig. 4.2) that were plotted to the right. This pattern seemed to be related to higher concentrations of H_3O^+-ions at the *natural forest* and *abandoned pasture low pH* compared to the other sites. The long arrow of this environmental variable pointed in the direction to the *natural forest* indicating that the soil pH was an important environmental factor in the PLFA ordination. In particular a higher relative abundance of the fatty acid cy19:0 typical of Gram-negative bacteria was found for the *natural forest*. Conversely to the arrow of H_3O^+, arrows of total organic C, total N and P pointed in opposite direction to the *active* and *abandoned pasture* site.

When focusing on the comparison of the microbial properties between *abandoned pasture* and *abandoned pasture low pH,* the above-described patterns were highlighted. In contrast to the similar amounts of PLFA ($PLFA_{tot}$) in 0–5 cm soil depth of both abandoned pasture sites, the microbial community structure seemed to be significantly different (Table 4.2). At the *abandoned pasture low pH* the relative abundance of Gram-negative bacteria as well as of actinomycetes were significantly higher whereas the relative fungal abundance was significantly lower (Table 4.2).

Table 4.2: Comparison of total PLFAs and specific microbial groups between both abandoned pasture sites (0–5 cm, mean, SE). Significant differences are indicated by different letters (Tukey test, $p<0.05$).

	n	**$PLFA_{tot}$**		**Gram(+)**		**Gram(-)**		**Actinomycetes**		**Fungi**	
		[nmol g^{-1}]		---------- [mol%] ----------							
abandoned pasture	*11*	94	(12)	15	(1)^{a}	39	(1)^{a}	5.5	(0.2)^{a}	6.0	(0.5)^{b}
abandoned pasture low pH	*4*	70	(7)	17	(1)^{b}	47	(3)^{b}	7.3	(0.7)^{b}	3.4	(0.6)^{a}

4.3 Response of soil microbes to bracken-invasion



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4.4 Response of soil microbes and pasture grass to fertilization

Hamer, U., Potthast, K., Makeschin, F., 2009. Urea fertilisation affected soil organic matter dynamics and microbial community structure in pasture soils of Southern Ecuador. Applied Soil Ecology 43, 226-233.

Since the article Hamer et al. (2009) is protected by copyright, please use the following internet link: http://dx.doi.org/10.1016/j.apsoil.2009.08.001

Potthast, K., Hamer, U., Makeschin, F., 2012. In an Ecuadorian pasture soil the growth of *Setaria sphacelata*, but not of soil microorganisms, is co-limited by N and P. Applied Soil Ecology 62, 103-114.

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5 Discussion

5.1 Impact of land-use changes

5.1.1 Soil CO_2 fluxes

In addition to the large flow of C from land to atmosphere by slash and burn of natural forest (Houghton, 2003), this study demonstrated that conversion of mountain rainforest to pasture land increased the C transfer from soil to atmosphere significantly. Annually about 2 Mg CO_2-C per hectare were additionally emitted at the *active pasture* site (12.2 Mg CO_2-C ha^{-1} a^{-1}) (Potthast *et al*., 2011). In the lowland tropics distinct patterns of soil CO_2 fluxes were observed. Compared to the adjacent primary rainforest, increases (Feigl *et al*., 1995b; Fernandes *et al*., 2002) as well as decreases (Davidson *et al*., 2000) of in situ soil respiration rates were measured on established pastures, making a general prediction of terrestrial ecosystem C transfers difficult. In the present study, higher soil CO_2 fluxes at the *active pasture* were mainly related to significantly higher levels of fine-root respiration and turnover rates. Since abandoned pastures still emit similar soil CO_2 fluxes as active ones (Potthast *et al*., 2011), it is crucial to find strategies for pasture re-establishment and afforestation to avoid further increases in C-inputs to the atmosphere by deforestation and newly established pastures.

5.1.2 Microbial structure and function

The land-use change from forest to pasture as well as inappropriate pasture management in combination with severe bracken-invasion was associated with an alteration in substrate quality entering the soil above- and belowground (Potthast *et al*., 2010, 2011). These changes in the quality of residue inputs influenced soil microbial function (amount and activity) and structure in different ways, severely impacting C and nutrient dynamics. Soil microbes mainly depended on two drivers: (i) resource availability (Bardgett and Wardle, 2010; Dijkstra *et al*., 2006) and (ii) soil chemical properties (soil pH, exchangeable cations) (Bååth and Anderson, 2003; Rousk *et al*., 2010a). Investigations along the land-use gradient revealed that the microbial structure and function responded independently of each other to changed soil environmental conditions.

A disconnection between microbial structure and function was found for *active* and *abandoned pasture* soil (Potthast *et al*., 2011). A decreased microbial activity and biomass due to decreased C and nutrient availability did not cause significant changes in the microbial

community structure after pasture abandonment (Fig. 5.1). The nearly unaltered microbial structure was shown to be associated with similar soil pH (Potthast *et al*., 2011). On a continental scale soil pH was a better predictor of the bacterial community structure than vegetation, C and nutrient availability or soil moisture (Fierer and Jackson, 2006). In a study along a land-use gradient in the southern US, Lauber *et al*. (2008) investigated that especially the bacterial community was influenced by soil pH. The abundance of Acidobacteria increased whereas that of α-Proteobacteria decreased with decreasing soil pH. In contrast, the fungal community was more strongly affected by substrate availability (Rousk *et al*., 2010a). The authors related this different response of bacteria and fungi to different ranges of pH optima for optimal growth. Based on these observations it was assumed that a further decrease in soil pH at abandoned pastures of the present study would also alter the structure of the soil microbes as shown in several studies (Bååth and Anderson, 2003; Rousk *et al*., 2010b; Thoms *et al*., 2010).

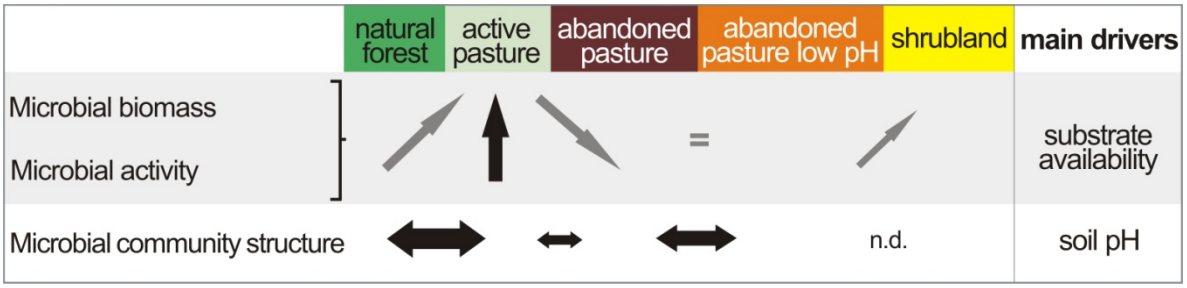

Figure 5.1: Response of microbial function (amount and activity) and structure (PLFA analysis) as well as their main drivers along the land-use gradient in the study area. The size of the arrows indicates the intensity of the microbial response; arrows faced upwards or downwards represent increases or decreases, respectively; no change is displayed by = sign. n.d.: not determined.

In the present study, the microbial community structure was significantly influenced by changed soil pH values. Increasing soil acidity at the *abandoned pasture low pH* (pH 4.1 in 0-5 cm) induced a shift in the microbial community structure assuming an adaption of the soil microbes. The pH value of this pasture site was below a threshold value of microbial properties at pH 4.5 which was detected by Rousk *et al*. (2009) along an in situ pH gradient (pH 8.3–3.3) of a grassland soil. It was found that the relative importance of fungi increased markedly (50-fold) below pH 4.5 (Aciego Pietri and Brookes, 2009; Rousk *et al*., 2011). However, Rousk *et al*. (2010a) detected a general decrease in the microbial activity and biomass, independent of their microbial group. Toxic conditions for soil microbes with increasing soil acidity due to an enhanced metal (Al, Zn, Cu) solubility could be one reason for this observation (Flis *et al*., 1993). In case of the present pasture soil, specific microbial groups, such as fungi, decreased in their abundance and others, like actinomycetes, increased while total microbial biomass was maintained. Thus, it seems likely that other microbial groups with functionally similar traits acceded the function of diminished groups at

higher soil acidity as a form of functional redundancy (Allison and Martiny, 2008; Paterson *et al*., 2009).

By contrast with the microbial structure and despite a difference of more than one pH unit, no relation between the soil microbial biomass and pH was detected considering all study sites along the land-use gradient. Thus, the microbial amount was not primarily influenced by soil pH. Thus, other factors seemed to be responsible for the difference in the microbial biomass. A multiple regression analysis taking into account further soil properties (SOC, TN, DOC, DON, TDN) showed that the microbial biomass C was positively correlated with the total soil nitrogen content. Soil nutrient resources, such as nitrogen, seemed to be an important factor of microbial growth in the study area. Since soil phosphorus content was not determined at all sites, its effect on the overall soil microbial biomass could not be affirmed along the land-use gradient, but has to be taken considered as a further important microbial limiting element. Higher amounts of microbial biomass (0–5 cm) at the *natural forest* and *shrubland* than at the *abandoned pastures* may be related to higher inputs of easily available substrates from the organic layer (Potthast *et al*., 2011) and due to higher throughfall-inputs of nutrients via leaching from leaves and dry depositions (Michalzik *et al*., 2001; Wilcke *et al*., 2001). At the *active pasture* site, the dense fine-root system of the *Setaria*-grass with its continuous delivery of easily available substrate (root-exudates) to soil microbes seemed to be mainly responsible for the highest soil microbial biomass and activity compared to all other sites (Potthast *et al*., 2011; Rhoades *et al*., 2000). In Section 5.2 this pattern is discussed in more detail.

An overview of the soil microbial response (structure, function) to land-use changes, as covered in the present study, is illustrated in Figure 5.1. In consideration of the soil microbial structure of the *abandoned pasture low pH*, the assumption of a disconnection between microbial structure and function corroborate the results of Section 4.1 where only the sites of *natural forest*, *active pasture* and *abandoned pasture* were investigated (Potthast *et al*., 2011). A specific sensitivity of the soil microbes to shifts in their community structure due to increasing or decreasing soil pH values within a range of pH 4.2 to 4.9 was found for the conversion from *natural forest* to *active pasture* and from the *abandoned pasture* to the *abandoned pasture low pH* site, respectively. Above and below this pH range, differences in the community composition were less pronounced along the land-use gradient. In contrast, the function of the microbial biomass was more influenced by differences in nutrient availability being highest at the *active pasture* site.

5.2 Soil fertility loss of pastures -reasons and first prevention steps-

Higher levels of SOM turnover rates at the newly established pasture indicated beneficial conditions for plant nutrient availability. However, results of the present study implied pasture use and infestation of bracken to have detrimental impacts on pasture soil fertility with the result of reduced pasture productivity. A decrease in SOM-quality was observed in the mineral top soil during pasture use and after pasture abandonment (Hamer *et al*., 2012a; Makeschin *et al*., 2008). At grazed pastures besides the selective C input via cattle dung (Clegg, 2006), most of the C is allocated belowground via grass roots and their exudates (Halliday *et al*., 2003; Rhoades *et al*., 2000). The suppression of the *Setaria*-grass, with its vigorously growing root system, by bracken reduced the belowground OM inputs to soil microbes and changed their soil environmental conditions. The ratios of C/N, C/P and N/P increased significantly (Hamer *et al*., 2012a; Makeschin *et al*., 2008) and the content of dissolved organic C (DOC) and NH_4-N (Hamer *et al*., 2009; Potthast *et al*., 2010) as well as the easily available PO_4-P pool (NH_4F extractable) decreased concomitantly by more than 50% (Hamer *et al*., 2012a). Plant productivity can be already limited by values of NH_4-F extractable PO_4-P below 15 mg kg^{-1} (Landon, 1991). At the pasture soils of the present study, determined values were lower than 5 mg kg^{-1} (0-5 cm) (Hamer *et al*., 2012a) which already indicated nutrient deficiency for grass growth. Setting fires on pastures heavily infested by bracken is common in the study area, but beneficial effects were only short-lived. Besides short-term increases in easily available substrates (personal observation), especially in inorganic P (Garcia-Montiel *et al*., 2000; Townsend *et al*., 2002), risks of nutrient losses due to volatilization and due to heavy rainfalls after fire will enhance nutrient limitation on the long run. Thus, pasture degradation will continue, increasing the areas of wasted land in the valley of Rio San Francisco.

The reduction in SOM, especially the decrease in nutrient availability, and changed environmental soil conditions after pasture abandonment were related to a decrease in the quality of above- and belowground OM inputs. These changes mainly altered soil microbial properties mediating SOM dynamics. In the following, C and nutrient cycling rates of *active* and *abandoned pasture* (dominated by bracken) top soils were compared, based on results from lab and field experiments, and consequences of pasture fertilization on SOM dynamics and on the quantity and quality of pasture grasses were examined.

5.2.1 Litter decay and SOM dynamics

The rate at which OM is mineralized by soil microbes depends, besides site-specific factors (temperature, moisture) and protection against microbial decay, mainly on the OM-chemistry (composition of functional polymers). The resource quality between grass and

bracken litter differed significantly. A two times higher C/N, C/P ratio, and lignin content was found for bracken litter. As was investigated by the in situ litterbag experiment (leaves: grass, bracken) about 81% of the grass litter has been decomposed during 17 months. In contrast, about 46% of bracken litter still remained after 17 months. The fast decay pool of the grass (63.6%) that was calculated according to a two-pool exponential decay model, was almost thrice as high as that of the bracken (21.9%) (Potthast *et al*., 2011). Thus, the pool of easily degradable molecular organic compounds of the bracken litter was more rapidly exhausted.

Both litter types differ in their chemical composition. Since individual chemical compounds differ in their relative decomposition rates (Leff *et al*., 2012; Rodeghiero *et al*., 2009), SOM accumulation may also be affected due to bracken-invasion. The addition of bracken litter to *active* and *abandoned pasture* soils did not affect the mineralization of native SOM in the first 20 days, whereas grass litter induced a retardation of native SOM mineralization (negative PE, 67–78%) (Potthast *et al*., 2010). The latter pointed to a preferential utilization of easily available organic substances derived from the grass litter. In both pasture soils, the mineralization of native SOM increased when the bracken litter derived substrate became exhausted from the 20th day on. During these later stages of incubation the microbial decomposition of bracken litter added to the *abandoned pasture* soil was N-limited. Furthermore, it could be assumed that the toxic ptaquiloside, which is a secondary metabolite during breakdown of bracken litter (Rasmussen *et al*., 2003), but not of grass, may has also influenced the bracken-decay. However, in the lab experiment bracken addition to pasture soils did not negatively influence soil microbial biomass. Furthermore, Engel *et al*. (2007) also found no impact of ptaquiloside on the overall soil microbial biomass, but rather a stimulation of their activity after the addition to bracken-infested soils in New Zealand and Denmark.

Generally, the microorganisms of the *active pasture* soil were the most active ones. There, the highest SOC and litter mineralization rates (C mineralization, gross N and net N mineralization) were detected in the short-term. The accumulation of SOM in the mineral topsoil of the *active pasture* was shown to be mainly driven by the high inputs of root biomass of the *Setaria*-grass (C_4 plant), using root- and shoot-specific molecular biomarkers (Hamer *et al*., 2012b). The fine root biomass of the *Setaria*-grass amounted up to 17.4 Mg C ha^{-1} in 0-10 cm depth (Potthast *et al*., 2011). The comparison of $\delta^{13}C$ values of the upper mineral soil between *active* and *abandoned pasture* soils also revealed that the SOC derived from the *Setaria*-grass was rapidly mineralized (within 10 years) after severe invasion of bracken (C_3-plant). Thus, high quality, N-rich organic substances derived from the *Setaria*-grass were preferentially mineralized by the soil microbes after pasture abandonment. Less degradable organic substances derived from bracken or from the former natural forest currently dominated the C-pool of the *abandoned pasture* soil leading to lower

turnover rates (Potthast *et al*., 2011) and to increased soil acidity in the upper mineral soil of specific abandoned pastures (*abandoned pasture low pH*, *shrubland*). This decrease in soil pH was associated with decreased concentrations of exchangeable Ca, K and Mg (Makeschin *et al*., 2008) as well as with an enhanced production of fulvic acids during decomposition of low-quality litter containing high proportion of phenolic acids (Swift *et al*., 1979). All these alterations were associated with a decrease in the microbial activity and growth leading to microbial amounts (MBC, $PLFA_{tot}$) being thrice as low as in the *active pasture* soil (Potthast *et al*., 2010, 2011).

In many parts of the world, the control of bracken is extremely difficult. Its vigorous rhizome system and high aboveground productivity are important traits in the easy displacement of pasture grasses (Marrs and Watt, 2006). In the study area, Roos *et al*. (2010b) examined two weed management strategies for the re-establishment of abandoned pastures overgrown by bracken. The first one was subjected to consecutive herbicide (picloram and metsulfuron methyl) treatments and the second one to cutting of bracken fronds every four months. Especially the allocation of nutrients in fronds and rhizomes is a successful trait of the bracken (Hartig and Beck, 2003; Killingbeck *et al*., 2002). As a consequence of this beneficial nutrient acquisition mechanism, pasture grasses can lose strength and can easily be reduced. The long-term allocation of nutrients in rhizomes can be a further reason for slower SOM mineralization rates and finally for the development of an organic layer found at the *shrubland* 20 years after abandonment. Energy and nutrients are no longer available for microbial mineralization and pasture production decreases leading to progressing pasture degradation. The comparison of nutrient concentrations in young and old fronds revealed a significantly higher concentration in young fronds (Tischer, unpublished results). Since litter decomposition of old bracken fronds was slow (Potthast *et al*., 2011), young fronds may be more rapidly mineralized releasing nutrients for grass growth. Thus, it is recommended to control bracken by cutting young bracken fronds before they get older and allocate their nutrients in their rhizomes (Tischer, unpublished results). Overall, these investigations emphasize the importance of an intensive bracken control already from the beginning of pasture establishment.

5.2.2 Fertilization and SOM dynamics

A fertilization experiment with nitrogen and/or phosphorus as major nutrients was conducted to test the hypothesis of plant and microbial nutrient limitation of active pastures. It was suggested that moderate fertilization can maintain or even improve soil fertility and thus enhance pasture productivity and quality. In particular, impacts of fertilization on SOM dynamics were examined.

Addition of urea was associated with a short-lived acceleration of SOM mineralization (real positive PE, 10–62% after 1 day) in the lab (Hamer *et al*., 2009). In the field, where the same amount of urea (50 kg N ha^{-1} a^{-1}/ 74 mg N kg dw soil) was applied, higher soil respiration rates were measured (**N**, **NP**) between the first and third day compared to the control (**X**) and rock phosphate amended treatment (**P**). These rates were also assumed to be related to additional short-term SOC-losses ranging between 0.6 (**NP**) and 0.8 (**N**) Mg CO_2-C ha^{-1} C annually (Potthast *et al*., 2012). In contrast to the litter entering the soil, the amended urea consist of simple available C (C/N_{urea}=0.4) that can be rapidly mineralized. Within one day between 78 to 81% of urea-C was released as CO_2 from the soil microcosms (Hamer *et al*., 2009). This urea addition induced a short-term abolishment of microbial nutrient and energy limitation where microbes were enabled to produce energetically expensive extracellular enzymes being able to mineralize SOM.

Extracellular enzymes produced by microbes are catalysts of OM decomposition and in turn may control soil microbial dynamics. Schimel and Weintraub (2003) stated that microbes will first use released C and nutrients for the synthesis of exoenzymes (N sink: $C/N_{protein}$=3), second to maintain their metabolism, and finally for their growth. It can be assumed that the first two microbial allocation priorities are more likely to dominate in the present soils, since no significant microbial growth and/or incorporation of nutrients were determined after urea amendment to *active* and *abandoned pasture* soil (lab and field experiment). In addition, net N mineralization instead of microbial N immobilization (gross NH_4 consumption rate) was found which was related to the lower C/N ratio of urea compared to the MBC/MBN ratio (<15). Only 22% N of total MBN in the soil was equivalently added by urea, thus the released N amounts in the lab may have been mainly used for the synthesis of N-rich exoenzymes. For example, proteolytic enzymes can produce low molecular weight (LMW) compounds, such as amides, amines or amino acids, through nutrient-mining in SOM. These LMW compounds can be used by soil microbes as energy source or as a building block for protein synthesis leading to their rapid turnover and gaseous SOC-losses (Nannipieri and Eldor, 2009).

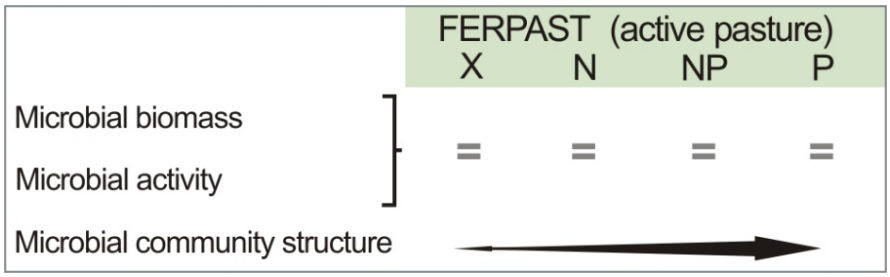

Figure 5.2: Response of microbial function (amount and activity) and structure (PLFA analysis) on fertilization of an *active pasture* (FERPAST). The size of the arrows indicates the intensity of the microbial response; and no change is represented by the = sign.

Microbes of the *active pasture* soil are not primarily limited by N and/or P. Instead, an altered nutrient availability due fertilization changed their community structure (Hamer *et al*., 2009; Potthast *et al*., 2012). The microbial community structure shifted towards a higher relative abundance of Gram(-) bacteria and saprophytic fungi, while neither the microbial biomass nor the immobilization of microbial N and P was affected (see also Fig. 5.2). Gross N mineralization rates between control (**X**) and urea-treated (**N**, **NP**) soil did not differ 14 days after fertilization which may also be related to the competitive strength of the pasture grass *Setaria sphacelata* (Potthast *et al*., 2012). As a consequence of an intensive microbe and plant interaction, increased nutrient availability due to rapid nutrient mineralization by soil microbes may have favored the competitiveness of the *Setaria*-grass for inorganic N uptake. In the field, grass productivity as well as fodder quality increased significantly after the combined fertilization of urea and rock phosphate (Potthast *et al*., 2012). A higher biomass and an increased concentration of P and Ca in the *Setaria*-grass were detected. According to the difference method by Syers *et al*. (2008) the *Setaria*-grass took up an equivalent of about 43% and 69% of added N and P, respectively, in their aboveground biomass annually. The belowground storage of N and P in grass roots was not verified.

Three years of moderate urea fertilization showed a slight decrease in the soil pH of the upper mineral soil which was counterbalanced when rock phosphate was additionally supplied (Potthast *et al*., 2012). These higher hydronium ion concentrations in the soil solution may originate from enhanced nitrification rates and/or from the release by plant roots as substitute for NH_4^+. The Ca ions derived from the rock phosphate may have buffered the soil solution (27 kg Ca ha^{-1} a^{-1}). Thus, a combined fertilizer use is recommended to prevent soil acidification processes.

In summary, although soil microbes responded with an adaptation of their structure to the increased short-term substrate availability after fertilization (urea and/or rock phosphate), their initial functions did not change in the long-term. By contrast, short-term priming effects were observed in the lab as well as in situ. Despite these short-term effects, the overall impact on soil C-cycling rates can be significant. For instance, accelerated gaseous losses of CO_2-C as well as potentials of soil acidification due to intensive urea additions alone have to be taken into account when establishing a sustainable pasture management in the study area. The greatest benefit of grass productivity was obtained after combined fertilization of urea and rock phosphate. Not only the grass quantity, but also its quality was improved.

5.3 Conclusions and Perspectives

Today, land-use changes are mainly proceeding in humid tropical regions where deforestation is associated with a huge loss of biodiversity and C from the ecosystems. Moreover, the established agricultural land frequently degrades rapidly and leads to large areas of wasted land. In the study area, about 18% additional soil CO_2-C fluxes were emitted annually at both pasture sites (active and abandoned) compared to the forest. In addition, further continuously higher ecosystem C outputs to the atmosphere would be induced by deforestation and increasing areas of newly established pastures. As a consequence, a rehabilitation of degraded pastures is a prerequisite to a sustainable land-use in the valley of Rio San Francisco.

The altered terrestrial C and nutrient dynamics are particularly related to a complex network of interrelations between soil microorganisms and their abiotic soil environment. A growing body of research work addresses the influence of resource availability and geochemical properties on soil microbial properties. Still, the specific processes addressing the relationships between microbial structure and function in the context of varying land-use changes are still not fully understood (Franklin and Mills, 2009). Rather little is known about the impact of land-use and vegetation changes on soil microbial properties in tropical mountain regions. The present study showed that patterns in microbial function and structure along the land-use gradient were distinct from each other, depending on the intensity of alterations in resource availability and soil environmental properties, respectively. Inappropriate pasture use and the invasion of bracken resulted in resource-limited conditions for microbial metabolism and growth. After pasture abandonment, with C, N and P availability decreasing but soil pH remaining on a similar level, microbial structure and function were disconnected in their response. It can be concluded that keeping only the soil pH above 4.9 would not improve soil quality on these sites, since the microbial biomass and activity was mainly affected by resource availability at the abandoned pasture. Thus, to maintain soil fertility on active pastures and to re-establish abandoned pastures the maintenance of or increase in resource availability for soil microbes will play an important role for grass growth and finally for pasture productivity.

The impact of land-use and vegetation change on the microbial structure was several orders of magnitude higher than that of pasture fertilization (urea and/or rock phosphate) (see Figure 5.3ab). As displayed in Figure 5.3b in which the effect of fertilization was also included in the RDA analysis, a greater shift of the soil microbial community structure was observed for land-use changes. This was mainly due to the soil environmental conditions having been more influenced by land-use changes leading to greater responses of the soil microbial community (Figure 5.3b). Thus, to make statements on the process-based

impact on the soil microbial community composition, the gradient of alterations in soil environmental conditions must be kept in mind, especially when comparing with other studies.

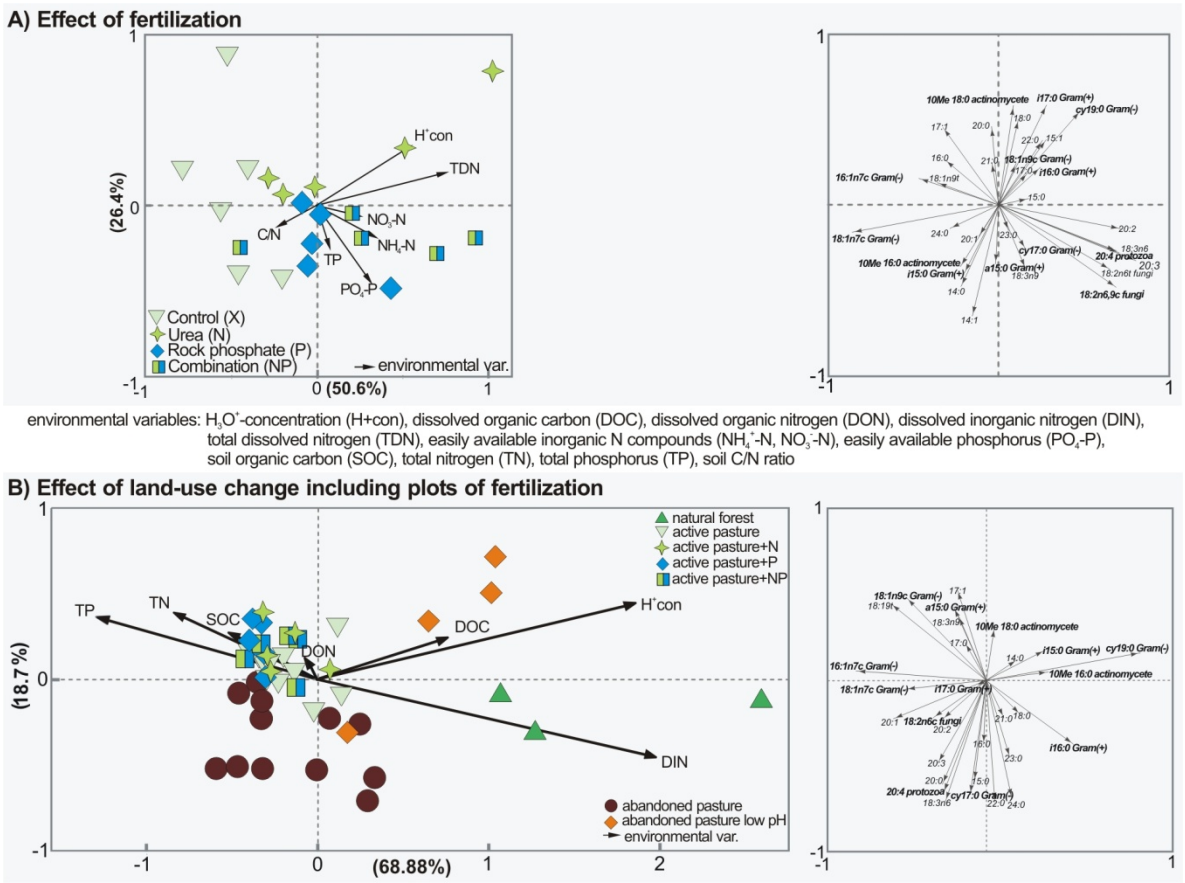

Figure 5.3: Comparison of two redundancy analyses comprising the soil microbial community structure (PLFA in mol%) and biogeochemical variables at 0–5 cm soil depth differing in their gradients of alteration. A) RDA of the effect of pasture fertilization (FERPAST) (Potthast *et al*., 2012), and B) effect of land-use change including the fertilized plots of FERPAST.

In the study area, pasture management practices that retain SOM in the long-term are required to provide nutrients for pasture grasses. The maintenance of the nutrient concentration in the soil solution, as one indicator of soil fertility, is important for the continuous supply with nutrients for grass growth (Mengel *et al*., 1999). The microbially mediated release of inorganic N and P into the soil solution is of high importance due to the fact that the main N- and P-pools of the studied pasture soils were in organic forms (Hamer *et al*., 2012a). Since soil fertility decreased rapidly during pasture use and abandonment (Hamer *et al*., 2012a; Makeschin *et al*., 2008), it was hypothesized that already at *active pasture* sites both soil microbes and pasture grass were nutrient-limited. However, only the latter hypothesis was confirmed. In particular, a co-limitation of the *Setaria*-grass by N

and P was observed after fertilization with urea and/or rock phosphate. In contrast, soil microbes were neither limited by N nor by P at the *active pasture*. Furthermore, as a consequence of detected short-term gaseous SOC losses as well as of soil acidification after urea application only, moderate urea fertilization in combination with rock phosphate is highly recommended. It can be assumed that a decline in soil pH to values lower than 4.2 has important implications on the soil microbial structure leading to decreased SOM dynamics which would be counterproductive for grass growth. Nevertheless, the quantity and quality (higher Ca and P content) of pasture grass was improved significantly after the combined fertilization. Especially for growing calves and lactating cattle a high fodder quality is essential and, in addition, the nutritional value of the milk can be improved (Subcommittee on Dairy Cattle *et al*., 2001). Thus, an application of moderate fertilizer loads of urea and rock phosphate can benefit pasture productivity. It can be considered as a first step towards a prevention of pasture degradation in the long-term and towards the strengthening of livestock health of the current stocking rate. However, it has to be taken into account that higher amounts of urea fertilizer could increase the risk of gaseous SOC and urea-N losses as well as soil acidification at the studied pasture soils. Additionally, in Ecuador increasing demand for milk and meat (FAO, 2009) will increase the stocking rates and/or the weight of the respective cattle. These measures do not only increase the fodder demand, but may also increase the risk of severe soil compaction, which was not found at present, with stocking rates of less than one cow per hectare. As a result of a severe soil compaction, the risk of soil fertility loss will aggravate (e.g. oxygen deficiency for microbes and plants).

Although the present experiment showed that fertilization is beneficial for pasture productivity, it cannot be the only solution for a sustainable land-use in the study area, since e.g. P-fertilizer is a non-renewable resource, suggested to be depleted within one century assuming current usage rates (Vaccari and Strigul, 2011). This P resource scarcity as well as rising prices for overall fertilizer production, especially for its energy consumption, will increase costs for farmers when using fertilizer. Thus, further solutions to reduce nutrient losses, to improve growth efficiency (efficient nutrient use, facilitated nutrient acquisition) and to recycle nutrients (closed nutrient cycles) are needed (Vance and Chiou, 2011). However, further research is required to test the establishment of P-solubilizing microorganisms (phosphatase or organic acid production) and mycorrhiza as well as the usage of cultivars with adapted root systems (cluster roots) or exudation strategies to mine soil nutrients which are not directly available for plant uptake (Vance *et al*., 2003; Wrage *et al*., 2010).

As a perspective for the pasture management in the valley of Rio San Francisco besides the use of specified grass species (such as *Setaria*) that are adapted to the prevailing climatic conditions, the combined planting with legumes is recommended to reduce the use

of synthesized nitrogen fertilizer. These legumes have to be adapted to the site-specific environmental conditions and have to be competitive against grass species. It is assumed that the combined planting with *Setaria* may be difficult since it could suppress the legumes. Investigations about the rehabilitation of abandoned pastures overgrown by bracken, encompassing tests of bracken control and fertilization, are still in progress in the study area.

To apply the results of the present study to other regions of the global biodiversity hotspots, such as “Mesoamerica” (all countries of Central America) and “Tropical Andes” (Venezuela, Colombia, Ecuador, Peru, and Bolivia) ('t Mannetje *et al*., 2008; Myers *et al*., 2000) several requirements have to be fulfilled: (i) conversion of mountain rainforest for pasture use (1,000-3,000 m asl), (ii) prevailing of Dystric Cambisols, (iii) 365 growing days, and (iv) perhumid climate. In the future, the focus and challenge will be on the restoration of ecosystem services of degraded pastures and abandoned areas to a sufficiently productive state aiming at the protection of the still prevailing natural forest ecosystem. With regard to a benefit-cost analysis of fertilization, further research is required to test its financial feasibility for pasture improvement, pasture restoration or for afforestation of abandoned pastures in the study area.

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Erklärung

Hiermit versichere ich, dass ich die vorliegende Arbeit ohne unzulässige Hilfe Dritter und ohne Benutzung anderer als der angegebenen Hilfsmittel angefertigt habe; die aus fremden Quellen direkt oder indirekt übernommenen Gedanken sind als diese kenntlich gemacht worden. Bei der Auswahl und Auswertung des Materials sowie bei der Herstellung des Manuskriptes habe ich Unterstützungsleistungen von folgenden Personen erhalten:

Weitere Personen waren an der geistigen Herstellung der vorliegenden Arbeit nicht beteiligt. Insbesondere habe ich nicht die Hilfe eines oder mehrerer Promotionsberater(s) in Anspruch genommen. Dritte haben von mir weder unmittelbar noch mittelbar geldwerte Leistungen für Arbeiten erhalten, die im Zusammenhang mit dem Inhalt der vorgelegten Dissertation stehen.

Die Arbeit wurde bisher weder im Inland noch im Ausland in gleicher oder ähnlicher Form einer anderen Prüfungsbehörde zum Zwecke der Promotion vorgelegt.

Ich bestätige, dass ich die Promotionsordnung der Fakultät Umweltwissenschaften der TU Dresden anerkenne.

…….
Ort, Datum

…….
Unterschrift (Vorname Name)

Curriculum vitae

Dipl. Geogr. Karin POTTHAST

PERSONALIA

Date of birth:	September 17, 1981
Place of birth:	Karl-Marx-Stadt (now Chemnitz), Germany

EDUCATION

PhD study

Since Jan 2007	Research Assistant at the Institute of Soil Science and Site Ecology, Dresden University of Technology , Germany
	PhD study within the DFG Research Unit FOR 816 „Biodiversity and Sustainable Management of a Megadiverse Mountain Ecosystem in South Ecuador“, subproject B 2.1 (Hamer / Makeschin) „Organic matter and microbial community structure“
	„*Implications of land-use change and pasture management on soil microbial function and structure in the mountain rainforest region of southern Ecuador*“
Oct – Nov 2011	Visiting scientist, Department of Chemistry, Division of Organic Chemistry, Wood, Pulp and Fiber Chemistry, University of Natural Resources and Life Sciences, Vienna, Austria: Pyrolysis-GC-MS analyses of soil fractions with different densities
Mar 2009	Summer School „Soil organic matter – composition and turnover“, Freising, Germany
2007 – 2011	Several research stays in Ecuador at the research station “Estación Científica San Francisco“ (11 months in total)

Study

Nov 2006	Graduation (Dipl.-Geogr.)
Oct 2005 – Jun 2006	Diploma thesis at the Institute of Soil Science and Site Ecology, Dresden University of Technology: „*Soil respiration dynamics and quantification of specific soil C fractions along a land-use gradient in the mountain rainforest region of southern Ecuador*“
Sept 2004 – Mar 2005	Research stay in Ecuador for the diploma thesis

2000 – 2006 Study of Geography, Dresden University of Technology, Germany
Subsidiary subjects: 1) Soil Science and Soil Protection
2) Waste Management and Contaminated Site Treatment

School

1992 – 2000 Grammar school, Samuel-von-Pufendorf-Gymnasium, Flöha

PUBLICATIONS

SCI-Publications

Potthast, K., Hamer, U., Makeschin, F. (2012): In an Ecuadorian pasture soil the growth of *Setaria sphacelata*, but not of soil microorganisms, is co-limited by N and P. Applied Soil Ecology 62, 103-114.

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Book chapters

Hamer, U., Potthast, K., Wilcke, W., Wullaert, H., Valarezo, C., Sandmann, D., Maraun, M., Scheu, S., Homeier, J. (2013): Future regulating (supporting) services: Matter turnover and nutrient additions. In: Bendix, J., Beck, E., Bräuning, A., Makeschin, F., Mosandl, R., Scheu, S., Wilcke, W. (eds.): Ecosystem Services, Biodiversity and Environmental Change in a Tropical Mountain Ecosystem of South Ecuador. Ecological Studies Vol 221, Springer, Berlin. (in Press)

Wilcke, W., Boy, J., Hamer, U., Potthast, K., Rollenbeck, R., Valarezo, C. (2013): Current regulating (supporting) services: Nutrient Cycle. In: Bendix, J., Beck, E., Bräuning, A., Makeschin, F., Mosandl, R., Scheu, S., Wilcke, W. (eds.): Ecosystem Services, Biodiversity and Environmental Change in a Tropical Mountain Ecosystem of South Ecuador. Ecological Studies Vol 221, Springer, Berlin. (in Press)

Roos, K., Bendix, J., Curatola, G., Gawlik, J., Gerique, A., Hamer, U., Hildebrandt, P., Knoke, T., Meyer, H., Pohle, P., Potthast, K., Thies, B., Tischer, A., Beck, E. (2013): Current provisioning services: Pasture development and use, weeds (bracken) and management. In: Bendix, J., Beck, E., Bräuning, A., Makeschin, F., Mosandl, R., Scheu, S., Wilcke, W. (eds.): Ecosystem Services, Biodiversity and Environmental Change in a Tropical Mountain Ecosystem of South Ecuador. Ecological Studies Vol 221, Springer, Berlin. (in Press)

Beck, E., Bendix, J., Silva, B., Rollenbeck, R., Lehnert, L., Hamer, U., Potthast, K., Tischer, A., Roos, K. (2013): Future provisioning services: Repasturisation of abandoned pastures, problems and pasture management. In: Bendix, J., Beck, E., Bräuning, A., Makeschin, F., Mosandl, R., Scheu, S., Wilcke, W. (eds.): Ecosystem Services, Biodiversity and Environmental Change in a Tropical Mountain Ecosystem of South Ecuador. Ecological Studies Vol 221, Springer, Berlin. (in Press)

Further publications

Beck, E., Roos, K., Hamer, U., Potthast, K., Tischer, A., Brenner, S., Bendix, J. (2012): Ecological aspects of repasturisation of abandoned mountain pastures in South Ecuador. In: Bräuning, A., Richter, M., Peters, T. (Eds.): Islands in land- and seascape: The challenges of fragmentation. Conference of the Society of Tropical Ecology. 22-25 February 2012, Erlangen. ISBN 978-3-00-037462-3.

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Tischer, A., Potthast, K., Hamer, U. (2011): Effects of DOM on mineralization processes and microbial community structure in managed and abandoned pasture soils in Southern Ecuador. In: Chronakova, A., Simek, M., Kyselkova, M., Hynst, J., Baldrian, P., Pospisek, M., Kristufek, V., Elhottova, D. (Eds.): Ecology of Soil Microorganisms – Book of abstracts. Prague April 27 - May 1 2011, 384 pp.

Potthast, K., Hamer, U., Makeschin, F. (2011): Implications of land-use change and pasture fertilization on soil microbial activities and communities in a mountain rainforest region of Southern Ecuador. In: Niekisch, M., Streit, B. (Eds.): Status and future of tropical biodiversity. Conference of the Society of Tropical Ecology. 21-24 February 2011, Frankfurt a. M. ISBN 978-3-89973-000-5.
Potthast, K.; Hamer, U. (2011): From forests to pastures: Soil respiration & microbial biomass. In: TMF-Newsletter No. 11 - DFG-Research Unit 816.

Potthast, K., Hamer, U., Makeschin, F. (2008): Impact of litter quality on mineralization processes in top soils of South Ecuador. In: Blum, W. H., Gerzabeck, M. H., Vodrazka, M. (Eds.). Book of Abstracts - Eurosoil 2008.

Oral presentations

DBG Workshop "Bodenmikroorganismen und ihre Rolle im Landnutzungswandel: Indikatoren, Prozesse und Bewertung" 2012, Tharandt:
Potthast, K., Hamer, U., Makeschin, F. (2012): Landnutzungswandel und Düngung beeinflussen Mikroorganismen in Böden der tropischen Bergregenwaldregion Ecuadors.

Status symposium of the DFG research unit (FOR 816) 2011, Loja, Ecuador:
Potthast, K., Hamer, U., Makeschin, F. (2011): Effect of pasture fertilization on soil quality and biomass production.

Tagung der Deutschen Bodenkundlichen Gesellschaft 2011, Berlin:
Potthast, K., Hamer, U., Makeschin, F. (2011): Weidedüngung in einer ecuadorianischen Bergregenwaldregion – Möglichkeit der Degradationsminderung?

Conference of the Society for Tropical Ecology (gtö) "Status and Future of Tropical Biodiversity" 2011, Frankfurt a. M.:
Potthast, K.; **Hamer, U.; Makeschin, F.** (2011): Implications of land-use change and pasture-fertilization on soil microbial activities and communities in a mountain rainforest region of Southern Ecuador.

Workshop "Regulation of soil organic matter and nutrient turnover in agriculture" 2009, Witzenhausen (University of Kassel):
Potthast, K.; **Hamer, U.; Makeschin, F.** (2010): Impact of litter quality on mineralization processes in managed and abandoned pasture soils in Southern Ecuador.

International conference of the "European Geoscience Union" 2010, splinter meeting, Vienna:
Potthast, K.; **Hamer, U.; Makeschin, F.** (2010): Response of soil microbial activity and community structure to land-use changes in a mountain rainforest region of Southern Ecuador.

Poster presentations

EUROSOIL 2012, Bari:
Potthast K., **Tischer, A., Hamer, U., Makeschin, F.** (2012): Importance of priming effects (PEs) for pasture management in Southern Ecuador.

EUROSOIL 2012, Bari:
Tischer A., **Potthast, K.,** **Hamer, U.** (2012): P and N availability constrains soil microorganisms and drives nutrient cycling and plant productivity in the tropical mountain rainforest region of Southern Ecuador.

EUROSOIL 2012, Bari:
Tischer A., **Potthast, K., Hamer, U.** (2012): Effects of plant-derived DOM on mineralization processes and microbial community structure in managed and abandoned pasture soils in Southern Ecuador.

International Conference "Ecology of Soil Microorganisms - Microbes as Important Drivers of Soil Processes" 2011, Prague:
Potthast, K., **Hamer, U., Makeschin F.** (2011): Land-use change and pasture-fertilization affects soil microorganisms and nutrient cycling in a tropical mountain rainforest region of Southern Ecuador.

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15th world conference on "Humic Substances & Natural Organic Matter" 2010, Tenerife (Canary Islands):
Potthast, K., **Hamer, U., Makeschin, F.** (2010): Impact of litter quality on mineralization processes in managed and abandoned pasture soils in Southern Ecuador.

International Conference "Organic matter stabilization and ecosystem functions" 2010, Presqu'île de Giens (Côte d'Azur):
Hamer, U., **Potthast, K.,** **Makeschin, F.** (2010): Priming effects in pasture soils of Southern Ecuador.

International Conference "Organic matter stabilization and ecosystem functions" 2010, Presqu'île de Giens (Côte d'Azur):
Potthast, K., Hamer, U., Makeschin, F. (2010): Implications of land-use change and pasture-fertilization on soil microbial activities and communities in a mountain rainforest region of Southern Ecuador.

International Conference "Organic matter stabilization and ecosystem functions" 2010, Presqu'île de Giens (Côte d'Azur):
Tischer, A., Potthast, K., Hamer, U., (2010): Mechanisms of organic carbon se-questration in pasture soils along management chronosequences in the South Ecuadorian Andes.

International conference of the "European Geoscience Union" 2010, Vienna:
Potthast, K., Hamer, U., Makeschin, F. (2010): Response of soil microbial activity and community structure to land-use changes in a mountain rainforest region of Southern Ecuador.

Tagung der Deutschen Bodenkundlichen Gesellschaft 2009, Bonn:
Potthast, K., Hamer, U., Makeschin, F. (2009): Einfluss der Streuqualität auf Mineralisierungsprozesse in Oberböden Südecuadors.

International Summer School "Soil organic matter -composition and turnover 2009", Freising:
Potthast, K., Hamer, U., Makeschin, F. (2009): Organic matter turnover and microbial community structure in soils of different land-use in the mountain rainforest region of South Ecuador.

EUROSOIL 2008, Vienna:
Potthast, K., Hamer, U., Makeschin, F. (2008): Impact of litter quality on mineralization processes in top soils of South Ecuador. In: Blum, W. H., Gerzabeck, M. H., Vodrazka, M. (Eds.). Book of Abstracts - Eurosoil 2008.

Tagung der Deutschen Bodenkundlichen Gesellschaft 2007, Dresden:
Potthast, K., Iost, S., Burneo, J.I., Makeschin, F. (2007): Dynamics of soil respiration and quantification of soil microbial characteristics along a land-use gradient in a mountain rainforest region of South Ecuador.